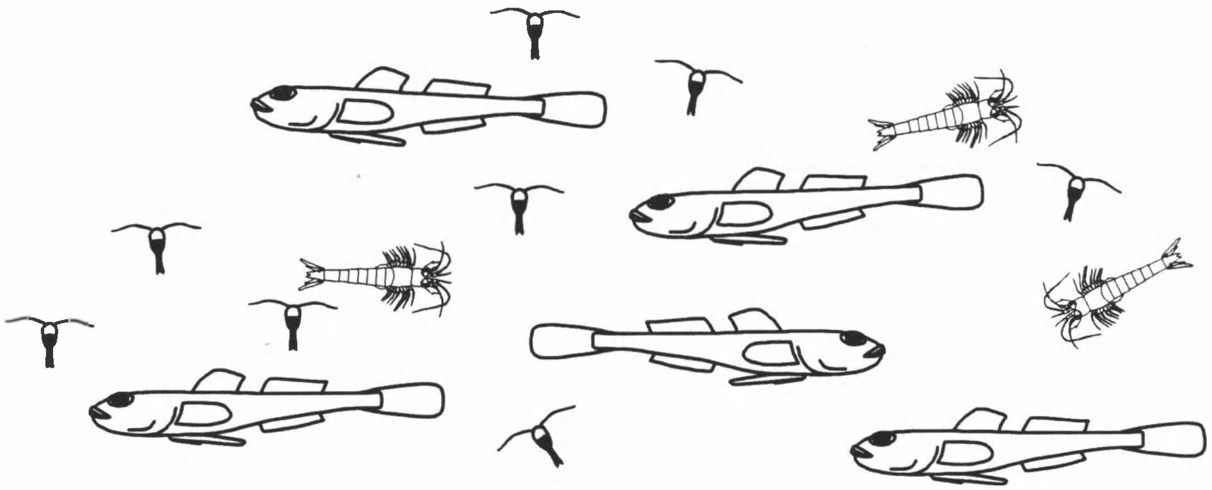
Universiteit Gent
Faculteit der Wetenschappen
Vakgroep Morfologie, Systematiek en Ecologie
Academiejaar 1992-1993

Instituut voor Dierkunde
Sektie Mariene Biologie

The ecology of *Pomatoschistus minutus* Pallas and *Pomatoschistus lozanoi* de Buen (Pisces, Gobiidae) in the shallow coastal waters and estuaries of the Southern Bight of the North Sea



by Olivier Hamerlynck

Promotor: Prof. Dr. C. Heip

Verhandeling voorgelegd tot
het behalen van de graad van
Doctor in de Wetenschappen
Groep Dierkunde

for מו מו and אבּא who created me

for קרן who is the present

for אהרן who holds the future

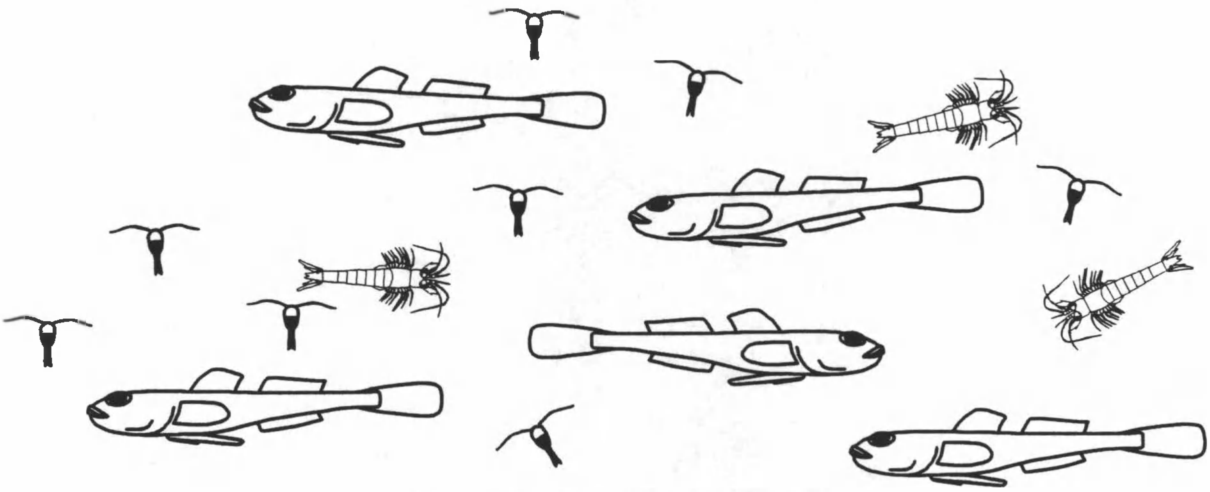
Leaders destroy the follower and the followers destroy the leader. Why should you have fate in anyone?

Jiddu Krishnamurti

Universiteit Gent
Faculteit der Wetenschappen
Vakgroep Morfologie, Systematiek en Ecologie
Academiejaar 1992-1993

Instituut voor Dierkunde
Sektie Mariene Biologie

The ecology of *Pomatoschistus minutus* Pallas and *Pomatoschistus lozanoi* de Buen (Pisces, Gobiidae) in the shallow coastal waters and estuaries of the Southern Bight of the North Sea



by Olivier Hamerlynck

Promotor: Prof. Dr. C. Heip

Verhandeling voorgelegd tot
het behalen van de graad van
Doctor in de Wetenschappen
Groep Dierkunde

for מר מר and אבא who created me

for קרן who is the present

for אהרן who holds the future

Leaders destroy the follower and the followers destroy the leader. Why should you have fate in anyone?

Jiddu Krishnamurti

TABLE OF CONTENTS

SUMMARY **1**

SAMENVATTING **5**

CHAPTER 1. The success of the Gobiidae: a short review of the recent literature **9**
Introduction 9
Global status of the Gobiidae 9
General biological features 10
Abundance 12
Trophic role 13
Gobiidae in various types of research 15
References 16

CHAPTER 2. The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands): Spatial structure **29**
Abstract 29
Introduction 30
Materials and methods 31
  Study area 31
  Sampling 32
  Environmental variables 33
  Multivariate analysis of community structure 35
  Terminology 36
Results 36
  Species composition 36
  Spatial structure 38
    Classification 39
    Characterisation of the species assemblages 39
    Relation to environmental variables 43
    Diversity 47
Discussion 48
Conclusions 51
Acknowledgements 52

CHAPTER 3. The identification of *Pomatoschistus minutus* (Pallas) and *Pomatoschistus lozanoi* (de Buen) (Pisces, Gobiidae) **53**
Abstract 53
Introduction 53
Material and methods 54
Results and discussion 54
  Pomatoschistus minutus 55
  Pomatoschistus lozanoi 56
Summary 58
Acknowledgements 59

CHAPTER 4. The parasites of two sympatric gobies *Pomatoschistus minutus* and *Pomatoschistus lozanoi* in the Belgian coastal waters . . . 61
Abstract . . . 61
Introduction . . . 61
Materials and methods . . . 62
Results . . . 62
Discussion . . . 64
Conclusions . . . 66
Acknowledgements . . . 66

CHAPTER 5. The trophic position of *Pomatoschistus lozanoi* (Pisces, Gobiidae) in the Southern Bight . . . 67
Abstract . . . 67
Introduction . . . 67
Materials and methods . . . 68
Results . . . 69
Discussion . . . 73
Acknowledgements . . . 75

CHAPTER 6. Daily ration of juvenile *Pomatoschistus lozanoi* de Buen (Pisces: Gobiidae). Influence of circadian, circatidal and semilunar rhythms. . . . 77
Abstract . . . 77
Introduction . . . 77
Materials and methods . . . 79
  Study area . . . 79
  Sampling . . . 80
  Calculation of daily ration . . . 82
Results . . . 84
Discussion . . . 87
Conclusions . . . 91
Acknowledgements . . . 92

CHAPTER 7. *Mesacanthion diplechma* (Nematoda: Thoracostomopsidae), a link to higher trophic levels? . . . 93
Abstract . . . 93
Introduction . . . 93
Results . . . 94
Discussion . . . 96

CHAPTER 8. The food of *Pomatoschistus minutus* (Pisces, Gobiidae) in the Belgian coastal waters, and a comparison with the food of its potential competitor *P. lozanoi* . . . 99
Abstract . . . 99
Introduction . . . 99
Materials and methods . . . 100
Results . . . 105
Discussion . . . 110
Acknowledgements . . . 115

CHAPTER 9. Differences in food resource use and competition in two species of Gobiidae *Pomatoschistus minutus* and *Pomatoschistus lozanoi* in a shallow coastal area 117
Abstract 117
Introduction 117
Materials and methods 118
Results 123
Discussion 129
Acknowledgements 136

CHAPTER 10. Growth, feeding, production and consumption in 0-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow coastal area of the SW Netherlands 137
Abstract 137
Introduction 138
Materials and methods 138
  Study area 138
  Sampling 140
  Stomach analysis 141
  Growth, mortality, production and consumption 141
Results 144
  Growth, density and spatial distribution 144
  Mortality 146
  Production 146
  Feeding and food consumption 147
Discussion 149
Acknowledgements 152

IMPLICATIONS 153

PREDICTIVE EPILOGUE 157

REFERENCES 159

APPENDIX 185

Foreword

When in early 1984 my promoter Carlo Heip suggested I should work on the trophic role of non-commercial fish I was a bit taken aback. Coming from a background in optimal foraging in birds, where you could sit back and watch how they handled every food item, I was appalled by the massive slaughter of fish for stomach analysis that, from the literature seemed a prerequisite for such research. Moreover, I had very little affinity with fish ecology. My only previous experience with fish was back in childhood. After persistent parent harassment we were allowed to keep a goldfish in a small aquarium on the window sill. As we continuously tried to overfeed it, we observed how it died from fungal disease in its eutrophicated surroundings.

One of the aims of the non-commercial fish project was to assess the importance of meiofauna as a food source for higher trophic levels. Besides of its obvious scientific interest, finding an important link from meiofauna to higher trophic levels would be a major asset in the permanent struggle for funds the Marine Biology Section of the Zoology Institute was engaged in. At the time it was certainly a hot topic and little could we know that several groups of Swedish researchers had a mountain of papers (as usual mostly a cyclic permutation of the same data) submitted, in press or in preparation on the topic. Our ignorance was perhaps fortunate because, as they were dealing with very shallow tranquil non-tidal environments covered by ice for part of the year, they could just walk out there in summer, drop some kind of device and come up with absolute density and biomass estimates of both predators and prey. Moreover, they had the whole dark and cold winter when sampling was unnecessary to deal with the summer samples. We could of course not know that some of their findings would be contradictory e.g. Evans (1984) stated that mobile epifauna consumed about 1 % of meiofauna production while in the next bay Pihl (1985) found they were taking 72 % of harpacticoid and ostracod production (Gee 1989). Though conceptually we were going to try to do the same thing the logistic constraints in our area were a bit different. The first problem was obtaining fish, preferably quantitatively and regularly. Belgium at the time did not even have a research vessel and the Fisheries Research Institute in Ostend only went collecting twice a year with a hired shrimp trawler for the Demersal Young Fish Survey. During these trips they had too much other work to collect non-commercials, anaesthetise them and store them in formalin. Also, it was exceedingly difficult to obtain permission to join these sampling trips. The obvious alternative was to restrict our research to some habitat where things would evidently be very different from the 'real' North Sea. A second point was that doing this type of research on your own would be quite hard. Most of the biologists from my graduation class were unemployed at the time and one of the most enthusiastic and capable among these (now Dr.) Colin Janssen was prepared to join the quest for gobies, which, because of their high abundance, were beginning to emerge as the first subject of study. Prof. Coomans was easily persuaded to spend a substantial percentage of the funds of the Institute on the acquisition of a small beam trawl and we could start pulling the thing over sandy beaches. After several unsuccessful trips and a lot of sweating we finally succeeded in catching 8 gobies on 10 May 1984. They did not seem to be nearly as abundant as was stated in the literature and most of our trips ended with between 0 (most common) and a meagre 5 or 10 fish per day. It was also clear that my genotype and phenotype were not very well adapted to beam trawling. Fortunately the team got a lot of help from Wim De Cock, another unemployed biologist of considerable talent who now writes computer programmes for a major bank. The fascinating thing was that 99 % of the gobies we caught seemed to be *Pomatoschistus lozanoi*, a species previously unknown from the Belgian coastal area. However, the identification of these animals is very difficult unless you know someone to teach you a few tricks. During the British Ecological Society meeting at Reading (4 Belgian scientists sharing a room with a single bed to reduce costs), the greatest of the great of international gobydom Dr. Peter J. Miller from the University of Bristol graciously picked me up at the station, confirmed our tentative identifications, taught me all the tricks, let me chat to his research students, served me an excellent meal accompanied by a perfect white wine and after some very pleasant conversation drove me back to the station.

As the sandy beach trawls never yielded a statistically sound sample, not even when we attended beam trawling competitions and snatched away the gobies from the bewildered competitors, we also started sampling in the Spuikom of Ostend, the Dievegat and, thanks to Guido Burggraeve, in the Zwin nature reserve. Most of these samples yielded only *Pomatoschistus microps* but in sufficient numbers. In the meantime however, the family connections of Colin Janssen yielded a new source of genuine coastal gobies in enormous quantities. Luk Bogaert, a commercial shrimp fisherman allowed us to collect as many gobies as we could carry and these are the cornerstone of the present thesis (chapters 4, 5, 7 and 8). However, by the end of 1985 the Belgian government decided that marine science was not a research priority and I joined my voluntary collaborators on the dole, which meant continuing the same work but for less pay.

The disadvantages of the commercial trawler samples were that no estimate of fish density could be made and that in spring the trawlers switched to sole fishing. Thanks to an introduction by Dr. Rudy Herman to the Rijkswaterstaat

Meetdienst Vlissingen a quantum leap in goby collecting was achieved. Director Jim Gossé and his successor Dick den Hoed warmheartedly supported the research for many years and provided us with virtually unlimited logistics. Moreover, all levels of the organisation participated with equal enthusiasm, the coordinators of the sampling trips Chris Scheers and Jan van Dijke, the skippers and crews of the various vessels, the technical workshop under the direction of Jo van Ieren and even the divers who from time to time had to disentangle the gear from obstacles or the propeller of the vessel. Special mention should be made of skipper Wim Goedegebuere who took the research to heart, spared nothing to make the hauls as accurate as possible, often invented things that improved the sampling and pulled the wagon when everything tended to go wrong (often). The 24-hour samplings with him and his crew were a pleasure (except that they were horrible) and the paper 'Daily ration of juvenile *Pomatoschistus lozanoi* (Pisces: Gobiidae). Influence of circadian, circatidal and semilunar rhythms' (chapter 6) is a tribute to them.

As the research could not go on building on volunteers and that team building seemed a prerequisite, the regular interval sampling with Rijkswatersaat allowed me to take on the responsibility of M.Sc. thesis students. The two first victims were Rik van Landtschoote (now running the mainframe of an important Japanese car manufacturer) and Dré Cattrijsse who has discreetly but forcefully sustained Goby Systems ever since. Dré also wrote an unforgettable computer programme that speeded up the analysis of stomach content data tremendously.

One of the remarkable aspects of the gobies was the importance of Mysidacea in their food and, as we thought gobies were important in the food chain so must be the mysids. The difficulty lay in sampling these creatures. Dr. Rudy Herman drafted a design for an epibenthic sledge and Rijkswaterstaat Meetdienst Vlissingen kindly built it. Thanks to Drs. Aad C. Smaal at the Rijkswaterstaat Dienst Getijdewateren some money became available for research into the role of hyperbenthic animals within the framework of the Voordelta project. After an initial phase with Rik van Landtschoote, this project was taken over by Peter van de Vyver (now writing computer programmes for tax evasion schemes for a major transnational) and Jan Mees. These two were always prepared to identify and measure thousands of animals at short notice and must have worked at least twice the number of hours they were paid for. Thanks to unrelenting support by Carlo Heip and the Netherlands Institute for Ecology, Centre for Estuarine and Marine Ecology (NIOO-CEMO) at Yerseke, and with financial backing from the EEC-MAST programme, the mysid business became a major topic in itself and is now in the dexterous hands of Jan Mees. In parallel with the hyperbenthic research Kris Hostens made an M.Sc. on the gadoids of the Voordelta and has remained an indispensable link in the group ever since, often on short-term shoestring budget contracts. Besides of their own research he and Dominiek Decleyre keep our computer systems working. Their help was indispensable.

The next step was expanding the research spatially. Thanks to the Dutch Academy of Sciences I became visiting scientist at the then Delta Institute for Hydrobiological Research, now NIOO-CEMO. The virtually unlimited logistic support of this institute was instrumental for chapters 2, 3, 7, 9 and 10 and an increasing number of other publications not included in this thesis. Many people have cooperated on these projects since then. Special mention should be made of Hans Francke who, until he was assigned to other tasks recently, shouldered a lot of the practical work both in the sampling and by identifying and measuring thousands of gobies. Wim Röber, skipper of the Luctor, who does his best to make the samples as representative as possible. Piet the Koeijer who knows more about fishes and the sea than all of us put together and Co van Sprundel who keeps the engine going and is an excellent cook.

Acknowledgements

I would like to thank the following persons and institutions

My promoter Prof. Dr. Carlo Heip, who founded the non-commercial fish research group and who, through his successive career stages, always backed it strongly scientifically, logistically and financially.

Prof. Dr. A. Coomans, the Director of the Zoology Institute, who always supported me and gave me total freedom in the research.

Prof. Dr. M. Vincx, head of the Marine Biology Section for the identification of numerous *Mesacanthion diplechma*, tolerating my nasty character, serving excellent Chambertin wine and perfect deserts, and providing support where possible.

Prof. Dr. P.H. Nienhuis, head of the estuarine foodchains research group at the NIOO-CEMO, for his enthusiastic support of the fish and hyperbenthic research.

Prof. Dr. E. Kuyken, for counting migrating whimbrels during my preparation for the Pharmacology exam, and all that went before and came after.

Prof. Dr. Joseph E. De Roose, for his mentorship during many years. He is a living proof that intelligence, ethics and surgery are not necessarily incompatible.

Dr. Peter M.J. Herman for many free-wheeling discussions which sprouted numerous *ad hoc* hypotheses, all unproved.

Dr. Ann Vanreusel for sheltering me from thousands of hours of teaching undergraduate courses and with whom cooperation was pleasant and non-competitive.

Dr. Frank Redant of the Fisheries Research Institute at Ostend for some of the samples but especially for an open and friendly cooperation throughout.

Dr. Rudy Herman, whose help was especially important in the early stages.

Dr. Peter Aerts & Dominiek Decleyre for interesting and confusing discussions on goby morphodynamics.

Johan Craeymeersch who is always prepared to embark on recalculations of everything. His contribution is essential simply because his macrobenthic samples are taken in the neighbourhood of the fish samples and we regularly need his data at short notice for our crazy ideas. I hope someone takes over his monitoring duties soon and pays him for a year so he can finally write up.

Dirk Maertens formerly of the Fisheries Research Institute at Ostend and now at International Training and Contact, for many a pleasant sampling trip on board the Belgica and for taking over one of my lectures at short notice so I could get on with the writing.

Rony Huys for identifying most of the harpacticoids found in the stomachs.

Paul A. Van Damme and Gonda Geets who are proving that cooperation between research groups at different universities can happen.

Eddy Buyvoets, Bernard, Marc, Willy and the others of the sampling team of the Fisheries Research Institute, Ostend.

Rosette De Boever, Alex Braeckman, Guy De Smet and Dirk Van Gansbeke for technical support. Wies Gijselinck for more than that.

Eddy Eneman of the Sea Aquarium in Ostend for general support.

The skipper Luk Bogaert and crew of the O599 'Zeevogel' and later the O62 'Seabird 2' for their essential contribution, hospitality on board and teaching of the lingo.

Skipper and crew of the Luctor and of the various vessels of the Meetdienst Vlissingen.

Rijkswaterstaat Meetdienst Vlissingen for permanent support in many aspects of the research.

Rijkswaterstaat Dienst Getijdewateren for providing funds that allowed us to answer other questions than they posed.

The Royal Netherlands Academy of Arts and Sciences for allowing me to work as a visiting scientist at the NIOO-CEMO in Yerseke and for their logistic support, access to the library, etc.

The parents and family of Colin Janssen for excellent spaghettis, good carpenting and warm welcomes after chilling sampling trips.

Patrice, Dan, Marijke & PVS for their hopefully lifelong friendship.

Last but not least the various and fluctuating (former) members of Goby Systems Unltd. (slave department). Jan, Kris, Dré, Peter, Wim, Colin, Rik, Paul, Veerle, Veerle, Renato, Diedel, An DW, Zekeria, Christopher, Esther, Nancy & Hederick. For their enthousism, workaholism, alcoholism and other major and sometimes hidden -isms. Without them we could not have survived emotionally, logistically and scientifically.

K & A participated in the creation of this work as if all three of us were elements of a superorganism.

SUMMARY

This thesis presents some aspects of the ecology of two highly abundant small marine teleost fishes belonging to the family Gobiidae *Pomatoschistus minutus* Pallas 1770 and *Pomatoschistus lozanoi* de Buen 1923. In spite of their high abundance in the coastal waters of western Europe these two entities were only recognised as separate species in the early 1970's, but had previously occasionally been described as separate subspecies or separate forms. In the shallow coastal zone densities of these animals can reach several per square meter of sea floor (corresponding to several gram Asfree Dry Weight per m^2). The species are fast growing, mature within a year and are known to occur in the stomachs of a variety of piscivores. Therefore they can be expected to play an important role in the energy fluxes to higher trophic levels.

In a first part (Chapter 1) a short introduction is given to the Gobiidae. In a second part (Chapters 2, 3 and 4) some basic studies are presented on the occurrence of *P. minutus* and *P. lozanoi*, their identification and their parasites. A third part (Chapters 5,6,7 and 8) considers the food resource use by *P. lozanoi*, the 24-hour feeding rhythm and daily ration of *P. lozanoi*, a report on a freeliving nematode occurring in *P. minutus* stomachs and the food resource use of *P. minutus*. In a fourth part (Chapter 9) the interaction between *P. minutus* and *P. lozanoi* is considered. In a fifth and final part (Chapter 10) the contribution of *Pomatoschistus* species to the annual food consumption of two abundant gadoids is discussed. This is followed by a statement on the implications of the results and by a predictive epilogue. After the references a short Appendix follows where the regressions, used for the calculation of prey weights, are presented.

Chapter 1 provides a short overview of the recent literature which reaffirms the success of the gobies, both in number of species and in number of individuals. A short summary of the biological characteristics of the Gobiidae is given. Some of the factors thought to have contributed to the high diversity and high abundance (small size, shallow habitats, multiple spawnings and brood care) are discussed. Gobies serve as a link to higher trophic level animals of a broad taxonomic range. Because they are easily accessible they have also been used, and perhaps abused, in a variety of scientific investigations. This chapter takes a separate reference list because its contents differ strongly from the rest of the thesis.

Chapter 2 describes the different epifaunal communities occurring on the soft bottoms of the Dutch Delta and links these communities to the environment. *Re* gobies, it demonstrates that *P. minutus* and *P. lozanoi* are a major component of the epifaunal community of the shallow coastal zone and the adjacent estuaries. Though gobies are abundant in all the communities defined, an interesting result is that both species are TWINSPAN indicator species (at high cut levels, both for density and for biomass) for different communities. *P. lozanoi* is indicator species for the inshore stations of the Voordelta and, more specifically (in density terms only) for the ebb tidal delta of the former Grevelingen estuary. *P. minutus* is indicator species for the Oosterschelde. The species therefore differ in their use of certain habitats and it is thought the near absence of *P. lozanoi* from the Oosterschelde is caused by predation.

Chapter 3 is a practical guide to the identification of both species at different sizes and in different seasons. The difference in pigmentation pattern of small *P. minutus* and *P. lozanoi* is described.

Chapter 4 documents some of the more obvious parasites encountered when doing stomach analyses of the gobies. *P. minutus* and *P. lozanoi* share all these parasites, but prevalence and intensity of infection differ between the two species. The explanations put forward for the observed differences are largely speculative. Since the time of publication of this chapter, some of the species of parasites have been renamed and intermediate hosts have been discovered. The ecological aspects of the host-parasite relationships will be developed in the theses of the co-authors to this chapter.

Chapter 5 discusses the food resource use by *P. lozanoi* in the shallow coastal zone. The importance of hyperbenthic mysids (especially *Schistomysis spiritus*) in the food was an unexpected result. Other important items were the pelagic copepod *Temora longicornis* and the small juveniles of *P. minutus*. In August, both in 1984 and 1985, *P. lozanoi* switched to benthic feeding.

Chapter 6 documents the feeding rhythm of *P. lozanoi* over 24 hours. The original purpose was to obtain an estimate of daily ration (the amount of food an animal consumes per day), an important variable for the calculation of annual energy budgets. The results seemed simple enough, with a peak feeding around midnight and a daily ration of about 1% of body weight. However, when a second 24-hour cycle was analysed, peak feeding was still around midnight, but daily ration was about 5% of body weight. On the basis of observed patterns in the, presumably daily, growth rings in the otoliths, the hypothesis is put forward that the large difference observed in food consumption may be linked to the spring-neap cycle. Possibly, prey activity determines the feeding rate and therefore daily ration and growth. The study of daily growth rings in *Pomatoschistus* will be the subject of the thesis of one of the co-authors to the chapter.

Chapter 7 concerns an oddity, namely the consumption of a species of nematode by *P. minutus*. Nematodes are not normally an important element in fish diets and it would seem that the present observation was rather exceptional.

Chapter 8 presents the food resource use by the *P. minutus* caught in the same hauls as reported in chapter 5 for *P. lozanoi*. *P. minutus* takes a wide variety of foods but is predominantly a benthic feeder. The food resource use by both species is compared and overlap values and niche breadths are calculated. The results confirm the view that *P. lozanoi* is more specialised but for the aberrant benthic feeding in August. Data are also presented on the temporal pattern in the gonado-somatic index. This confirms the different spawning periods for *P. minutus* and *P. lozanoi*, already documented by other authors. In April, and to a lesser extent in May, *P. minutus* males have a lot of *Pomatoschistus* eggs in their stomachs. This presumably points to aggressive take-overs of spawning territories occupied by other males. Sneaker males, small males that look like females externally but have much larger testes than normal males, were found to occur in both species. Strangely the gonado-somatic index of *P. lozanoi* males is only about half that in *P. minutus*.

Chapter 9 deals with the difference in food resource use between the two species and with the possibility that the species may be competing for food. A simple field test is presented which investigates the pattern in resource use by the two species along a food-richness gradient in a snapshot comparative study. If interspecific competition caused the observed differences in food resource use, theory predicts that resource overlap should decrease when food becomes limiting. Such a pattern could not be demonstrated and it is therefore concluded that interspecific competition for food was probably not the causal mechanism of the observed difference.

Chapter 10 discusses production and consumption by two abundant 0-group gadoids, bib *Trisopterus luscus* and whiting *Merlangius merlangus*. Two different methods are used to estimate food consumption. In whiting, good agreement is found between the calculations based on stomach contents and those based on production and a Production:Consumption (P:C) ratio. Gobies account for 15 to 35 % of the annual consumption by the gadoids.

SAMENVATTING

Deze thesis behandelt enkele aspekten van de ekologie van twee talrijk voorkomende grondelsoorten: *Pomatoschistus minutus* Pallas 1770 en *Pomatoschistus lozanoi* de Buen 1923. Grondels zijn kleine mariene vissen (Teleostei) behorend tot de familie van de Gobiidae. Ondanks het feit dat beide soorten zeer abundant zijn langs de meeste Westeuropese kusten, werden ze tot in het begin van de jaren '70 niet als afzonderlijke soorten herkend. Af en toe werden ze wel als aparte ondersoorten of als verschillende vormen van dezelfde soort beschouwd. In de ondiepe kustzone kunnen deze dieren dichtheden bereiken van meerdere individuen per vierkante meter (wat overeenstemt met meerdere grammen Asvrij Drooggewicht per m^2). Het zijn snelgroeiende dieren die binnen het jaar geslachtsrijp worden. Bovendien worden ze vaak aangetroffen in de magen van allerlei viseters. Dit laat vermoeden dat ze een belangrijke rol spelen in de energiefluxen naar hogere trofische niveaus.

In een eerste deel (Hoofdstuk 1) wordt een korte inleiding gegeven tot de Gobiidae of grondels. In een tweede deel (Hoofdstukken 2, 3 en 4) wordt over enkele basisstudies gerapporteerd met betrekking tot het voorkomen van de beide grondelsoorten, hun identifikatie en hun parasieten. Een derde deel (Hoofdstukken 5, 6, 7 en 8) behandelt achtereenvolgens het gebruik van voedselbronnen door *P. lozanoi*, het 24-uurs voedingsritme van en de dagelijkse konsumptie door *P. lozanoi*, een anekdotisch verslag over het voorkomen van een bepaalde soort vrijlevende nematode in de magen van *P. minutus* en het gebruik van voedselbronnen door *P. minutus*. Een vierde deel (Hoofdstuk 9) gaat dieper in op de interakties tussen beide soorten, met nadruk op het mogelijk voorkomen van kompetitie voor voedsel. In een vijfde en laatste deel (Hoofdstuk 10) komt een aspekt van de energiestromen naar hogere trofische niveaus aan bod: het belang van grondels in het voedsel van enkele veel voorkomende kabeljauwachtigen. Dit alles wordt gevolgd door een stuk over de implikaties van het voorliggende werk en een epiloog. Na de referenties volgt nog een korte Appendix, waarin de voor het berekenen van de prooigewichten gebruikte regressies gerapporteerd worden.

Hoofdstuk 1 geeft een bondig overzicht van de recente literatuur over de Gobiidae. Dit herbevestigt de visie dat grondels een succesvolle diergroep zijn, zowel qua soortenrijkdom als qua aantallen individuen. Enkele van de faktoren waarvan vermoed wordt dat ze tot dit succes hebben bijgedragen, worden kort besproken: het kleine formaat van de meeste grondels, hun voorkomen in ondiepe habitaten, het feit dat ze meerdere keren eieren afzetten binnen één paaiseizoen en de broedzorg die ze aan die eieren besteden. Grondels zijn een voedselbron voor een taxonomisch diverse groep predatoren. Aangezien grondels gemakkelijk te vangen zijn en relatief weinig eisen stellen qua aquariumlogistiek zijn ze gebruikt, en misschien ook misbruikt, bij een hele reeks wetenschappelijke studies. De referentielijst van dit hoofdstuk is apart geplaatst omdat de inhoud van het hoofdstuk sterk verschilt van deze van de rest van de verhandeling.

Hoofdstuk 2 beschrijft de verschillende gemeenschappen van op de bodem levende dieren (epifauna) van de zachte substraten van het Deltagebied en het verband tussen deze gemeenschapsstruktuur en een aantal omgevingsveranderlijken. Met betrekking tot de grondels toont deze studie aan dat *P. minutus* en *P. lozanoi* inderdaad een hoofdkomponent uitmaken van de epifauna van het ondiepe kustgebied en de aangrenzende estuaria. Alhoewel grondels in alle beschreven gemeenschappen talrijk voorkomen, zijn er toch duidelijke verschillen in habitatgebruik tussen *P. minutus* en *P. lozanoi*. Dit wordt afgeleid uit het feit dat beide soorten indikatorsoorten zijn (in de TWINSPAN, de tweewegs indikatorsoorten analyse) voor verschillende gemeenschappen. Zo is *P. lozanoi* indikator voor de buitendelta van de Oosterschelde en voor deze van het voormalige Grevelingenestuarium. *P. minutus* is indikator voor de Oosterschelde zelf. *P. lozanoi* komt vrijwel niet voor in de Oosterschelde. Dit is vermoedelijk te wijten aan predatie.

Hoofdstuk 3 is een praktische determinatiegids die toelaat de twee soorten te onderscheiden. Het verschil in pigmentatiepatroon tussen de juvenielen van beide soorten wordt beschreven.

Hoofdstuk 4 behandelt een aantal van de meest opvallende parasieten van beide grondelsoorten. Het betreft enkel de parasieten die men bij maaganalyses vrijwel niet over het hoofd kan zien. Alle aangetroffen soorten parasieten kwamen bij beide grondelsoorten voor, maar zowel de prevalentie als de intensiteit van de infektie verschilden. De verklaringen die aangedragen worden voor deze verschillen zijn grotendeels spekulatief. Sinds de publikatie van dit hoofdstuk zijn een aantal van de parasieten aan een andere soort toegeschreven. Ook zijn inmiddels een aantal tussengastheren bekend. De ekologische aspekten van de gastheer-parasiet relaties van beide soorten zullen in de verhandelingen van de co-auteurs van dit hoofdstuk behandeld worden.

Hoofdstuk 5 bespreekt het voedsel van *P. lozanoi* in de ondiepe kustzone. Een onverwacht resultaat was het grote belang van aasgarnalen, voornamelijk *Schistomysis spiritus*, in het voedsel. Andere belangrijke voedselbronnen waren de planktonische copepode *Temora longicornis* en de kleine juvenielen van *P. minutus*. In augustus schakelt *P. lozanoi* plots over op het eten van benthisch voedsel.

Hoofdstuk 6 rapporteert over een onderzoek naar het 24-uurs voedingsritme van *P. lozanoi*. Oorspronkelijk was het de bedoeling om aan de hand hiervan de dagelijkse voedselkonsumptie te bepalen. Kennis hiervan is belangrijk om de jaarkonsumptie te kunnen schatten. Er werd een duidelijk voedingsritme gevonden met een piek rond middernacht. De berekende konsumptie bedroeg ongeveer 1% van het lichaamsgewicht van de vis per dag. Een tweede 24-uurscyclus toonde weer een piek rond middernacht maar nu was de berekende konsumptie bijna 5% van het lichaamsgewicht per dag. In the otolieten van grondels kan men ringen zien, waarvan het vermoeden bestaat dat ze dagelijks aangelegd worden. De otolieten vertonen gebandeerde patronen die telkens 14 ringen bevatten. Het grote verschil in voedselkonsumptie is mogelijk gebonden aan de springtij-doodtij cyclus. Het lijkt niet onmogelijk dat prooiaktiviteit het voedingsritme, en dus ook de dagelijkse konsumptie en groei, determineert . De groeiringen in de otolieten zullen het onderwerp vormen van de verhandeling van één van de co-auteurs van het hoofdstuk.

Hoofdstuk 7 dokumenteert een merkwaardige observatie over het voorkomen van een vrijlevende nematode in het voedsel van *P. minutus*.

Hoofdstuk 8 bespreekt het voedsel van *P. minutus*. Het betreft vissen die in dezelfde sleep gevangen werden als de *P. lozanoi* die in Hoofdstuk 5 besproken werden. *P. minutus* eet voornamelijk benthische prooien maar heeft een zeer ruime prooikeuze. Het voedselbronnengebruik van beide soorten wordt vergeleken en nichebreedte en -overlap worden berekend. De resultaten bevestigen dat *P. lozanoi* een meer gespecialiseerde soort is, als men abstraktie maakt van de aberrante voedselkeuze in augustus. Het seizoenaal verloop van de gonado-somatische index van beide soorten wordt ook besproken. De resultaten bevestigen de temporale scheiding van de paaiperiodes van beide soorten. In april, en in mindere mate ook in mei, worden in de magen van mannelijke *P. minutus* veel *Pomatoschistus* eieren aangetroffen. Dit wijst op het voorkomen van agressieve overnames van bezette territoria. Bij beide soorten werden mannetjes aangetroffen die gebruik maken van een alternatieve reproduktieve strategie. Deze kleine mannetjes hebben het uitwendig uitzicht van wijfjes, maar inwendig vertonen ze (voor grondels) uitzonderlijk grote testes. Merkwaardig genoeg is de gonado-somatische index bij *P. lozanoi* mannetjes maar half zo hoog als bij *P. minutus* mannetjes.

Hoofdstuk 9 gaat over het verschillend gebruik van voedselbronnen door de twee soorten en over de mogelijkheid dat dit verschil te wijten zou zijn aan kompetitie. Het patroon van voedselgebruik werd onderzocht langsheen een gradiënt in voedselrijkdom. Een voorspelling van het kompetitiemodel is dat, indien het voedsel meer limiterend wordt, de overlap tussen beide soorten zou moeten afnemen. Dit soort trend werd niet gevonden. Bijgevolg werd besloten dat kompetitie waarschijnlijk niet de oorzaak was van het verschillend gebruik van voedselbronnen.

Hoofdstuk 10 berekent het aandeel dat grondels uitmaken in de jaarlijkse konsumptie door juveniele kabeljauwachtigen. De jaarkonsumptie werd op twee manieren berekend: enerzijds vanuit de maaginhouden, anderzijds aan de hand van een produktieschatting en een produktie:konsumptie (P:C) ratio. Grondels maakten 15 à 30 % uit van de jaarkonsumptie door steenbolk en wijting.

Chapter 1

The success of the Gobiidae: a short review of the recent literature

INTRODUCTION

According to Hoese (1984) the Gobiidae belong with the Rhyacichthyidae (1 species, Pacific Island streams), Eleotridae (about 300 species, mostly freshwater and estuarine), Xenisthmidae (about 10 species, coral reefs), Microdesmidae (about 10 species, wormlike), and Kraemeriidae (about 8 species, buried in sand) to the Gobioidei, a suborder of Acanthopterygian teleosts. Though the Gobioidei are clearly monophyletic, their affinity to other Acanthopterygian orders is unclear. Many of the typical features of the suborder are negatively defined, i.e. the loss of certain bones and the reduction of the sensory canals (Akihito 1986). This makes them a difficult group for the application of traditional cladistic procedures. The relationships of the different families within the Gobioidei at present lack a phylogenetic basis and are currently under discussion (Springer 1983, Birdsong *et al.* 1988, Harrison 1989). Major advances in the understanding of Gobioid systematics can be expected from a wider application of biochemical techniques (e.g. El-Tawil 1984, Wallis & Beardmore 1984, Pezold & Grady 1989, McKay & Miller 1991).

In this paper the status and ecological role of the Gobiidae is reviewed. The emphasis is on literature from 1980 or later. Comparatively recent reviews which focus either entirely or predominantly on Gobioidea or Gobiidae are Miller (1979), Darcy (1980), Miller (1984).

GLOBAL STATUS OF THE GOBIIDAE

Judging from the number of species the Gobioidei are the most successful group of recent marine teleost fishes. About 1800 species of Gobioidei have been described to date (Miller 1986) and it is thought that some 2000 species may exist (Hoese 1984). This is roughly equivalent to the number of species in the Rodentia, which represent about half of all mammalian species. The vast majority of these species belong to the Gobiidae *sensu* Hoese (1984), which at present contains about 1600 species in 220 genera (Hoese 1986). Numerous additional species can be expected from, especially Indo-Pacific, coral reefs and mangrove systems (Hoese 1986). Even in European waters new species have still been discovered occasionally since 1980 (Miller 1981, Ahnelt & Bianco 1990, Economidis & Miller 1990, Miller 1992a).

GENERAL BIOLOGICAL FEATURES

The typical goby would be a small-sized fish (less than 15 cm) inhabiting shallow coastal marine or estuarine waters. Only a few exceptional species are found below 200 m depth (Birdsong 1988). The fusion of the pelvic fins into an adhesive disk allows the fish to remain stationary on the substrate in relatively strong currents. The group includes the smallest known vertebrates with adult sizes of less than 10 mm (Miller 1984, Winterbottom 1990). Size reduction allows efficient feeding on small prey and creates possibilities for the exploitation of spatially restricted habitats (Miller 1979). On the negative side, size reduction entails greater susceptibility to predation. Small Gobiidae have relatively higher brain weights than larger species and this is thought to relate to the increased predation pressure (Bauchot *et al.* 1989). Recent morphological studies include Mestermann & Zander (1984), Murdy (1985), Rojo (1985), Decleyre *et al.* (1990), Mehta *et al.* (1990) and Rouse & Pickles (1991). Development has been studied by Wyanski & Targett (1985) and Sunobe & Nakazono (1987). That the morphological concept of the Gobiidae is successful is exemplified by the independent evolution of goby-like morphologies in African cichlids (Yamaoka *et al.* 1986) and Antarctic Notothenioidea (Ekau 1991).

The reproduction (tokology) of gobioid fishes has been reviewed in Miller (1984). During the spawning season the male guards a suitable substrate on which the eggs are deposited. It seems likely that the sperm duct gland of the males, a synapomorphy of the Gobioidei (Miller 1992b), has some function related to the brood care exhibited by the males. The females are repeat spawners, laying relatively small batches of eggs several times per (extended) spawning season. However, gobies have developed many alternative lifestyles and show a wide adaptive radiation. Protogynic hermaphroditism seems to be widespread in at least some genera of Gobiidae (Robertson & Justines 1982, Fishelson 1989, Cole 1990, Sunobe & Nakazono 1990). Many species show progenetic (e.g. Winterbottom 1990) characters which may relate to the miniaturisation of Gobiidae from larger ancestors (Miller 1979).

It is thought the group has evolved in estuarine or shallow marine habitats. This contention is supported by the fact that most species have some form of brood care so typical for estuarine or shallow water species (Dando 1984). Their capacity to colonise riverine habitats of recent origin such as exist on Pacific islands (Ryan 1991), e.g. on Palau (Bright & June 1981) and Hawaii (Kinzie 1988) is also suggestive of a euryhaline past. Many riverine gobies have retained amphidromous characteristics (Mizuno 1980, Radtke *et al.* 1988) but other species complete their life cycle in fresh water. Some have developed specific adaptations to this environment e.g. the remarkable rock-climbing goby (Fukui 1979).

Very high diversities can be found on coral reefs, both in the Atlantic e.g. 46 species on Columbian reefs (Garzon Ferreira & Acero 1988) and the Indo-Pacific e.g. 90 species in the Chagos Archipelago, Central Indian Ocean (Winterbottom & Emery 1986). Gobiidae are the most diverse family in the Red Sea with over 85 species out of a total of about 1000 fish species (Goren 1986). Even in temperate areas diversity can be quite high e.g. 11 species in Loch Hyne, Ireland (Costello 1992, Wilkins & Myers 1992) and on a Japanese mud-flat (Kikuchi & Yamashita 1992). Some species have adapted to extreme environments e.g. *Pseudogobius olorum* living in hypersaline lakes at a salinity of 55 (Halse 1981). Other species have adapted to hypogean life in caves (Berti & Ercolini 1991). The remarkable Australian desert goby lives in, often saline, artesian springs (Miller 1987). The subfamily Oxudercinae (formerly Periophtalminae) or mudskippers comprises the most terrestrial of fishes (review in Murdy 1988). Much research has been done on their air-breathing capabilities (Iwata & Kakuta 1983, Natarajan & Rajulu 1983, Iwata 1988, Al-Kadhomiy & Hughes 1988, Low *et al.* 1988, Yadav *et al.* 1990) and some on its capabilities for terrestrial feeding (Sponder & Lauder 1981). Other groups of Gobiidae and Eleotridae can use aquatic surface respiration to cope with hypoxia (Gee & Gee 1991).

Many species are commensal with alpheid shrimp (Karplus 1987), others live inside sponges (Tyler & Böhlke 1972, Hoetje *et al.* 1977), associate with Echinoderms and Anthozoans such as corals (Goren & Diamant 1983, Goren 1986) and sea anemones (Hanlon *et al.* 1983) or are cleaner fish (Ehrlich 1975), both of fish (Johnson & Ruben 1988, Kerstitch 1984) and invertebrates (Johnson & Chase 1982). Some of these associations are obligatory, others are facultative. There is a record of an association between a species of Gobiidae and a Nudibranch mollusc (Williams & Williams 1986).

Many species make use of natural burrows e.g. of Nereid polychaetes (Sakai & Goto 1982), construct their own (Goren 1986, Yamaoko *et al.* 1991), use artificial ones e.g. empty beverage cans (Ogura & Kishi 1985) or associate with other burrowing animals such as alpheid shrimp (Karplus 1987), ghost shrimp *Calianassa* (Hoffman 1981) or *Nephrops* (Nash & Gibson 1982). In some species the burrow is only used during the spawning season (supposedly the primitive condition), other associations are permanent.

The estuarine and nearshore character of the group makes them ideal candidates for allopatric speciation through vicariant effects of sea level changes and the geomorphological dynamics of coastal areas: estuaries and marine bays can easily change into lagoons, then become lakes, and can much later be reunited with the open sea, possibly in a different zoogeographical region. Such a sequence of events is thought to lie at the basis of origin of the Mediterranean freshwater gobies with Ponto-Caspian affinities during the late Miocene Messinian salinity crisis (Miller 1990). Many other variants, leading to the isolation of goby populations and speciation can be imagined (McKay & Miller 1991).

The gastro-intestinal system, lacking a true stomach, is relatively simple even in herbivorous species (Geevarghese 1983), which are characterised by a long coiled intestine.

Dominance in near-shore and estuarine habitats, small size and euryhalinity have also contributed to the success of Gobiidae as invading species. Examples include transport in ballast water (Paxton & Hoese 1985) and accidental or intentional releases (Kopylets & Dukravets 1981, Miller 1984, Zerunian & Gandolfi 1986, Sokolov *et al.* 1989, Miller 1990, Mina 1992, Jude *et al.* 1992).

ABUNDANCE

Besides being a diverse group, adult Gobiidae can be very abundant and even dominant components of ecosystems. Examples are tidal pools in South Africa (Beckley 1985), sea grass beds in Japan (Azuma *et al.* 1983), tropical Australia (Blaber *et al.* 1992) and Texas (Huh & Kitting 1985), mangrove systems in Mexico (Maeda Martinez *et al.* 1982) and West Africa (Wright 1986), mussel rafts in Spain (Lopez-Jamar *et al.* 1984), soft bottoms on the west coast of Scotland (Nash & Gibson 1982), the Black Sea (Pinchuk & Savchuk 1982), the Baltic (Thorman & Wiederholm 1986, Zander & Döring 1989, Aarnio & Bonsdorff 1993) and coastal areas of the North Sea (Evans 1984, Hamerlynck *et al.* in press), estuaries in Europe (O'Sullivan 1984, Claridge *et al.* 1985), South Africa and Australia (Potter *et al.* 1990), saltmarshes in Australia (Morton *et al.* 1988) and Florida, where the impact of space shuttle launches on gobies has been investigated (Provancha & Hall 1991). The riverine *Rhinogobius similis* is so abundant that, according to Kopylets & Dukravets (1981), it competes with commercial species and requires control measures. Judging from the abundance of goby otoliths in Miocene deposits (Grenfell 1983, Brzobohaty 1989) the goby success story is already several million years old.

In spite of the relatively low batch fecundities: typically a few hundred to a few thousand eggs (Miller 1984), related to the small size of the adults and also characteristic for fishes exhibiting brood care, the small juveniles and larvae of a number of species dominate, or are an important component of, the ichthyoplankton of a wide range of habitats. Examples in Europe include Cadiz (Drake & Arias 1991) and Kiel Bay (Müller 1988). In southern Africa they dominate in estuaries (Harrison & Whitfield 1990), bays (Beckley 1986), surf zones (Whitfield 1989) and the upwelling area of the Namibian coast (Oliver & Rubies 1987). Examples from the Indo-Pacific include oceanic waters off Hawaii (Clarke 1991), coastal areas and saltmarshes of California (Edmands 1981, Leithiser 1981), India (Rengarajan & Raj 1985), and Australia (Jenkins 1986, Leis & Goldman 1987), mangrove systems in East Africa (Little *et al.* 1988) and Thailand (Janekarn & Boonruang 1986) and several areas along the western shores of the Pacific (Kim 1984, Hur & Yoo 1984, Belyanina 1987, Yoo & Cha 1988). In the Western Atlantic they dominate in a variety of inshore habitats from Chesapeake Bay through the Gulf of Mexico (Mendez Vargas 1980, Mihursky *et al.* 1981, Dokken *et al.* 1984, Houde & Lovdal 1984, Setzler-Hamilton 1987, Powell *et al.* 1989, Hettler & Chester 1990), down to Venezuela (Luckhurst & Powles 1981) and Brazil (Monteiro 1982). In most ichthyoplankton studies Gobiidae either come first or are second in abundance only to the larvae of Clupeoids, most commonly anchovies. Judging from the input of larvae the reproductive strategy of gobies seems to be quite successful. Reproductive effort in gobies takes up a large part in their total energy budget (Rogers 1988).

TROPHIC ROLE

At a time it was thought that part of the success of the Gobiidae could be explained by their (small size related) capacity to exploit the highly productive meiofauna (Miller 1979). Meiofauna as food for fish was reviewed by Gee (1989).

In some specific habitats meiofauna may be an important prey item for gobies (Bodiou & Villiers 1979, Fitzhugh & Fleeger 1985, Gee 1987, Aarnio & Bonsdorff 1993, Hamerlynck & Vanreusel in press) but most juvenile gobies have a planktonic life-style and depend mainly on zooplankton (e.g. Mehner 1992, Hamerlynck *et al.* submitted) at first. When they adopt a demersal life style they are usually large enough to consume small macrobenthic animals (Hamerlynck & Cattrijsse submitted) and meiofauna, though occasionally significant numerically (Gee 1987, 1989, Aarnio & Bonsdorff 1993, Hamerlynck & Vanreusel in press), are of minor energetic importance (Hamerlynck *et al.* 1990, Hamerlynck & Cattrijsse submitted).

Gobiidae are important links in the trophic chain to fish, birds, reptiles and mammals.

Gobies are a major prey group of gadoids of the central Adriatic (Granitto 1985), Norwegian fjords (Fosså 1991, Salvanes *et al.* 1992) and North Sea coastal areas (Hamerlynck & Hostens 1993). Young stages of important commercial flatfish species such as *Paralichthys olivaceus* (Nashida *et al.* 1984) are dependent on gobies. Gobies also feature prominently in the diet of piscivores in mangrove systems (Blaber 1986). They are important food for many estuarine fishes (Ramos-Porto & Vasconcelos 1980, Assis *et al.* 1992, Costa *et al.* 1992). They are also a dominant component in the food of that most precious of all fish, the Iranian sturgeon (Takami *et al.* 1980).

Pelagic gobies such as *Crystallogobius linearis* and *Gobiusculus flavescens* are dominant items in the food of overwintering Alcidae (Blake 1983). *Sufflogobius bibarbatus* is a dominant item in the food of penguins and cormorants in the Benguela upwelling ecosystem (Crawford *et al.* 1985, Duffy *et al.* 1987). Piscivorous ducks, grebes and cormorants depend on gobies in winter (Doornbos 1984). Even waders can feed on gobies (Warnock 1989).

Gobies are also important prey for sea snakes (Voris & Voris 1983). Gobies feature prominently in the diet of young seals shortly after weaning (Sievers 1989). For adult seals they are of lesser importance (Krylov 1984).

In spite of the small size of most species some Gobiidae are also directly consumed by humans, primarily in Asia (Wickstroem & Enderlein 1991), but also around the Mediterranean (Fabi & Froglia 1984) and the Black Sea (Pinchuk 1991) where some species are even cultured (Chepurnov 1989).

Their abundance and the importance of gobies in trophic links also makes them ideal candidates for parasite transfer. They are important intermediate hosts of *Botriocephalus* parasites of predatory fish (Robert *et al.* 1988, Zander & Döring

1989) and also play a role in the parasite transfer to fish eating birds (Zander & Döring 1989).

GOBIIDAE IN VARIOUS TYPES OF RESEARCH

Because of their abundance, accessability in near-shore waters and modest requirements on aquarium logistics, Gobiidae have been used for a variety of studies in ecotoxicology (Berge *et al.* 1983, Hose *et al.* 1984, Yazdandoust 1985, Oertzen *et al.* 1988, Fossi *et al.* 1989, Naess *et al.* 1991).

Karyological studies in fishes (review in Ozouf-Costaz & Foresti 1992) have mainly been confined to freshwater fishes and salmonids (Hartley & Horne 1984) but in the studies of marine fishes the Gobiidae are relatively well represented. Most Gobiidae examined have a diploid complement of 46 chromosomes (Webb 1986) and the evolutionary trend seems to be in the direction of fusion rather than dissociation of chromosomes (Thode *et al.* 1983). Several karyological studies have been done for the analysis of phylogenetic relationships (Webb 1980, Maldonado *et al.* 1985, Rab 1985, Webb 1986, Nayak & Khuda-Bukhsh 1987). Some authors have reported cytologically recognizable sex chromosomes (e.g. Pezold 1984), but because of the frequent occurrence of complex polymorphisms (Giles *et al.* 1985, Vitturi & Catalano 1989, Amores *et al.* 1990), their interpretation is controversial (Thode *et al.* 1988) and overt karyological heterogamy, if it exists at all, does not seem to be a common feature in the Gobiidae (Webb 1986). For the elucidation of phylogenetic relationships karyological studies are best used in conjunction with isozyme studies (Zhiqing & Ronqing 1987, McKay & Miller 1991).

Gobies have also been used extensively for ethological studies, especially of the fascinating breeding behaviour (Torricelli *et al.* 1985, 1986, Magnhagen & Kvarnemo 1989, Bisazza *et al.* 1989, Sunobe & Nakazono 1990, Magnhagen & Forsgren 1991, Lugli *et al.* 1992). Studies have also been done on predator avoidance (Kerstitch 1984, Magnhagen 1988, Smith & Smith 1989, Utne *et al.* 1993), home ranges (Azuma *et al.* 1988) and on combinations of predator avoidance and breeding behaviour (Magnhagen 1990, Magnhagen & Vestergaard 1991). The existence of satellite or sneaker males is well established (Cole 1982, Miller 1984, Hamerlynck & Cattrijsse submitted). It was suggested by Magnhagen (1992) that the sneaker strategy may be an ontogenetic phenomenon but this is challenged by Hamerlynck & Cattrijsse (submitted). The fish observed by Magnhagen (1992) were morphologically normal males while the sneaker males found in *P. minutus* and *P. lozanoi* have the external appearance of females (Hamerlynck & Cattrijsse submitted). Another remarkable feature is the production of alarm pheromones that are perceived both by conspecifics (Smith 1989) and other species (Smith *et al.* 1991). Some gobies can produce sound (Mok 1981, Torricelli *et al.* 1986).

Some endocrinological studies have been carried out in Gobiidae (Kulikova 1985, Moiseeva 1985, Iwata & Bern 1985, Lorenz & Assad 1986, Gray & Kelley 1991).

REFERENCES

Aarnio, K. & Bonsdorff, E. 1993. Seasonal variation in abundance and diet of the sand goby *Pomatoschistus minutus* (Pallas) in a northern Baltic archipelago. Ophelia 37: 19-30.

Ahnelt, H. & Bianco, P.G. 1990. *Orsinigobius milleri* n. sp., a new species of freshwater goby from W.-Greece (Pisces: Gobiidae). Annalen des Naturhistorisches Museums in Wien 90 B: 31-42.

Akihito, P. 1986. Some morphological characters considered to be important in gobiid phylogeny. In: Uyeno, T., Arai, R., Taniuchi, T., & Matsuura, K. (Eds.). Indo-Pacific fish biology. Proceedings of the second international conference on Indo-Pacific fishes: 629-639.

Al-Kadhomiy, N.K. & Hughes, G.M. 1988. Histological study of different regions of the skin and gills in the mudskipper, *Boleophthalmus boddarti* with respect to their respiratory function. Journal of the marine biological Association of the United Kingdom 68: 413-422.

Amores, A., Giles, V., Thode, G. & Alvarez, M.C. 1990. A tandem fusion in the fish *Gobius paganellus* (Gobiidae, Perciformes), a karyotypically polymorphic species. Genome 33: 57-59.

Assis, C.A., Almeida, P.R., Moreira, F., Costa, J.L. & Costa, M.J. 1992. Diet of the twaite shad *Alosa fallax* (Lacépède) (Clupeidae) in the river Tagus estuary, Portugal. Journal of Fish Biology 41: 1049-1050.

Azuma, M., Azeta, M. & Mitsumura, K. 1983. Shijiki-wan ni okeru madai wakauo to kyozon-gyoshu tono shokomotsu wo meguru shukan kankei. Bulletin of the Seikai Regional Fisheries Research Laboratory 59: 101-118.

Azuma, N., Sawara, Y., Hino, K. & Fukui, K. 1988. Kotaishikibetsuho ni yoru numachichibu (*Tridentiger brevispinis*) no kodo kansatsu. Hirosakidai Rika Hokoku (Scientific Reports of the Hirosaki University) 35: 22-30.

Bauchot, M.-L., Ridet, J.-M., Daigne, M. & Bauchot, R. 1989. Encephalization in Gobioidei (Teleostei). Japanese Journal of Ichthyology 36: 63-74.

Beckley, L.E. 1985. The fish community of East Cape tidal pools and an assessment of the nursery function of this habitat. South African Journal of Zoology 20: 21-27.

Beckley, L.E. 1986. The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. South African Journal of Zoology 21: 244-252.

Belyanina, T.N. 1987. Ichthyoplankton of the Gulf of Tonkin (composition, distribution and seasonal changes in populations). Journal of Ichthyology 27: 51-57.

Berge, J.A., Johannessen, K.I., Reiersen, L.-O. 1983. Effects of the water soluble fraction of North Sea crude oil on the swimming activity of the sand goby, *Pomatoschistus minutus* (Pallas). Journal of Experimental Marine Biology and Ecology 68: 159-167.

Berti, R. & Ercolini, A. 1991. *Caecogobius cryptophthalmus* n.gen. n.sp. (Gobiidae Gobiinae), the first stygobic fish from Philippines. Tropical Zoology 4 : 129-138.

Birdsong, R.S. 1988. *Robinsichthys arrowsmithensis* a new genus and species of deep-dwelling gobiid fish from the western Caribbean. Proceedings of the Biological Society Washington 101: 438-443.

Birdsong, R.S., Murdy, E.O. & Pezold, F.L. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. Bulletin of Marine Science 42: 174-214.

Bisazza, A., Marconato, A. & Marin, G. 1989. Male competition and female choice in *Padogobius martensi* (Pisces, Gobiidae). Animal Behaviour 38: 406-413.

Blaber, S.J. 1986. Feeding selectivity of a guild of piscivorous fish in mangrove areas of North-west Australia. Australian Journal of Marine and Freshwater Research 37: 329-336.

Blaber, S.J.M., Brewer, D.T., Salini, J.P., Kerr, J.D. & Conacher, C. 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, Northern Australia. Estuarine, Coastal and Shelf Science 35: 605-620.

Blake, B.F. 1983. A comparative study of the diet of auks killed during an oil incident in the Skagerrak in January 1981. Journal of Zoology 201: 1-12.

Bodiou, J.Y. & Villiers, L. 1979. La prédation de la meiofaune par les formes juveniles de *Deltentosteus quadrimaculatus* (Teleostei, Gobiidae). Vie Milieu 28-29: 143-156.

Bright, G.R. & June, J.A. 1981. Freshwater fishes of Palau, Caroline Islands. Micronesia 17: 107-111.

Brzobohaty, R. 1989. Die untermiozaene Otolithenfauna von Maigen bei Eggenburg, Niederösterreich. Annalen des Naturhistorisches Museums in Wien 90: 21-47.

Chepurnov, A.V. 1989. Kul'tivirovanie ryb Chernogo morya v zamknutykh sistemakh. Naukova Dumka, Kiev. 104 pp.

Claridge, P.N., Hardisty, M.W., Potter, I.C. & Williams, C.V. 1985. Abundance, life history and ligulosis in the gobies (Teleostei) of the inner Severn Estuary. Journal of the marine biological Association of the United Kingdom 65: 951-968.

Clarke, T.A. 1991. Larvae of nearshore fishes in oceanic waters near Oahu, Hawaii. NOAA Technical Report - NMFS 101. 26 pp.

Cole, K.S. 1982. Male reproductive behaviour and spawning success in a temperate zone goby, *Coryphopterus nicholsi*. Canadian Journal of Zoology 60: 2309-2316.

Cole, K.S. 1990. Patterns of gonad structure in hermaphroditic gobies (Teleostei: Gobiidae). Environmental Biology of Fishes 28: 125-142.

Costa, J.L., Assis, C.A., Almeida, P.R., Moreira, F.M. & Costa, M.J. 1992. On the food of the European eel, *Anguilla anguilla* (L.) in the upper zone of the Tagus estuary, Portugal. Journal of Fish Biology 41: 841-850.

Costello, M. 1992. Abundance and spatial overlap of gobies (Gobiidae) in Lough Hyne, Ireland. Environmental Biology of Fishes 33: 239-248.

Crawford, R.J.M., Cruikshank, R.A., Shelton, P.A. & Kruger, I. 1985. Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense perennial upwelling system. South African Journal of Marine Science 3: 215-228.

Dando, P.R. 1984. Reproduction in estuarine fish. In: Potts, G.W. & Wootton, R.J. (Eds.). Fish reproduction: strategies and tactics. Academic Press, London: 155-170.

Darcy, G.H. 1980. Comparison of ecological and life history information on gobiid fishes, with emphasis on the south-eastern United States. NOAA Technical Memorandum NMFS-SEFC-15: 1-53.

Decleyre, D., Aerts, P. & Verraes, W. 1990. On the functional significance of the dorsal part of the Aω muscle in *Pomatoschistus lozanoi* (Teleostei: Gobiidae). Belgian Journal of Zoology 120: 209-213.

Dokken, Q.R., Matlock, G.C. & Cornelius, S. 1984. Distribution and composition of larval fish populations within Alazan bay, Texas. Contributions in Marine Science 27: 205-222.

Doornbos, G. 1984. Piscivorous birds on the saline lake Grevelingen, the Netherlands: abundance, prey selection and annual food consumption. Netherlands Journal of Sea Research 18: 457-479.

Drake, P. & Arias, A.M. 1991. Composition and seasonal fluctuations of the ichthyoplankton community in a shallow tidal channel of Cadiz Bay (S.W. Spain). Journal of Fish Biology 39: 245-263.

Duffy, D.C., Wilson, R.P. & Wilson, M.P. 1987. Spatial and temporal patterns of diet in the Cape cormorant off southern Africa. Condor 89: 830-834.

Economidis,, P.S. & Miller, P.J. 1990. Systematics of freshwater gobies from Greece (teleostei: Gobiidae). Journal of Zoology 221: 125-170.

Edmands, F.A.II 1981. The dynamics of ichtyoplankton populations collected during dial sampling periods by stationary nets in upper Newport Bay, California. Estuaries 4: 277.

Ehrlich, P.R. 1975. The population biology of coral reef fishes. Annual Review of Ecology and Systematics: 211-247.

Ekau, W. 1991. Morphological adaptation and mode of life in high Antarctic fish. In: Di Prisco, G., Maresca, B. & Tota, B. (Eds.). Biology of Antarctic fish. Springer verlag, Berlin: 29-39.

El-Tawil, M.Y. 1984. Distribution of lactate dehydrogenase isozyme patterns of gobioid fishes. Bulletin of the Marine Research Centre Tripoli 5: 5-35.

Evans, S. 1984. Energy budgets and predation impact of dominant epibenthic carnivores on a shallow soft bottom community at the Swedish West coast. Estuarine, Coastal and Shelf Science 18: 651-672.

Fabi, G. & Froglia, C. 1984. A note on the biology and fishery of the black goby (*Gobius niger*) in the Adriatic Sea. FAO Fisheries reports 290: 167-170.

Fishelson, L. 1989. Bisexuality and pedogenesis in gobies (Gobiidae: Teleostei) and other fish, or, why so many little fish in tropical seas. Senckenbergiana maritima 20: 147-169.

Fitzhugh, G.R. & Fleeger, J.W. 1985. Goby (Pisces: Gobiidae) interactions with meiofauna and small macrofauna. Bulletin of Marine Science 36: 436-444.

Fosså, J.H. 1991. The ecology of the two-spot goby (*Gobiusculus flavescens* Fabricius): The potential for cod enhancement. ICES marine Science Symposia 192: 147-155.

Fossi, C., Leonzio, C. & Focardi, S. 1989. Meccanismi di detossificazione e fenomeni di adattamento in organismi marini. Oebalia 15: 885-891.

Fukui, S. 1979. On the rock-climbing behavior of the goby, *Sicyopterus japonicus*. Japanese Journal of Ichthyology 26: 84-88.

Garzon Ferreira, J. & Acero, P.A. 1988. Los peces Gobiidae de los arrecifes del Caribe Colombiano. 1. Especies, distribucion, frecuencia y abundancia. Annales del Instituto de Investigaciones Marinas de Punta de Betin 18: 59-81.

Gee, J.M. 1987. Impact of epibenthic predation on estuarine intertidal harpacticoid copepod populations. Marine Biology 96: 497-510.

Gee, J.M. 1989. An ecological and economic review of meiofauna as food for fish. Zoological Journal of the Linnean Society 96: 243-261.

Gee, J.H. & Gee, P.A. 1991. Reactions of gobioid fishes to hypoxia: Buoyancy control and aquatic surface respiration. Copeia 1991: 17-28.

Geevarghese, C. 1983. Morphology of the alimentary tract in relation to diet among gobioid fishes. Journal of Natural History 17: 731-741.

Giles, V., Thode, G. & Alvarez, M.C. 1985. A new Robertsonian fusion in the multiple chromosome polymorphism of a mediterranean population of *Gobius paganellus* (Gobiidae, Perciformes). Heredity 55: 255-260.

Goren, M. 1986. A suggested model for the recolonization process of the Red Sea at the post glacial period. In: Uyeno, T., Arai, R., Taniuchi, T. & Matsuura, K. (Eds.). Indo-Pacific fish biology. Proceedings of the second international conference on Indo-Pacific fishes: 648-654.

Goren, M. & Diamant, A. 1983. On the occurrence of *Tenacigobius yongei* (Davis & Cohen) in the Gulf of Elat (Red Sea) (Pisces: Gobiidae). Israel Journal of Zoology 32: 135-137.

Granitto, M.E. 1985. Osservazioni sull'alimentazione di *Antonogadus megalokynodon* (Kolombatovic) (Pisces; Gadidae) nel medio Adriatico. Quaderni dell'Istituto di Ricerca di Pesca Marittima, Ancona 4: 205-218.

Grenfell, H.R. 1983. Lower Miocene teleost otoliths from New Zealand. Bulletin of Marine Science 33: 779.

Gray, E.S. & Kelley, K.M. 1991. Growth regulation in the gobiid teleost, *Gillichthys mirabilis*: Roles of growth hormone, hepatic growth hormone receptors and insulin-like growth factor-I. Journal of Endocrinology 131: 57-66.

Halse, S.A. 1981. Faunal assemblages of some saline lakes near Marchagee, western Australia. Australian Journal of Marine and Freshwater Research 32: 133-142.

Hamerlynck, O. & Cattrijsse, A. (submitted). The food of *Pomatoschistus minutus* (Pisces, Gobiidae) in the Belgian coastal waters, and a comparison with the food of its potential competitor *P. lozanoi*.

Hamerlynck, O. & Hostens, K. 1993. Growth, feeding, production and consumption in 0-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow coastal area of the SW Netherlands. ICES Journal of marine Science 50: 81-91.

Hamerlynck, O. & Vanreusel, A. (in press). *Mesacanthion diplechma* (Nematoda: Thoracostomopsidae), a link to higher trophic levels? Journal of the marine biological Association of the United Kingdom.

Hamerlynck, O., Vyver, P. van de & Janssen, C.R. 1990. The trophic position of *Pomatoschistus lozanoi* (Pisces, Gobiidae) in the Southern Bight. In: Barnes, M. & Gibson, R.N. (Eds.). Trophic relationships in the marine environment. Proceedings of the 24th European Marine Biology Symposium. Aberdeen University Press, Aberdeen: 183-190.

Hamerlynck, O., Cattrijsse, A. & Arellano, R.V. (submitted). Daily ration of juvenile *Pomatoschistus lozanoi* (Pisces: Gobiidae). Influence of circadian, circatidal and semilunar rhythms.

Hamerlynck, O., Hostens, K., Arellano, R.V., Mees, J., Damme, P.A. van (in press). The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands): spatial structure. Netherlands Journal of Aquatic Ecology.

Hanlon, R.T., Hoxon, R.F. & Smith, D.G. 1983. Behavioral associations of seven West Indian reef fishes with sea anemones at Bonaire, Netherlands Antilles. Bulletin of Marine Science 33: 928-934.

Harrison, I.J. 1989. Specialization of the gobioid palatopterygoquadrate complex and its relevance to gobioid systematics. Journal of Natural History 23: 325-353.

Harrison, T.D. & Whitfield, A.K. 1990. Composition, distribution and abundance of ichthyoplankton in the Sundays River estuary. South African Journal of Zoology 25: 161-168.

Hartley, S. & Horne, M. 1984. Chromosome relationships in the genus *Salmo*. Chromosoma 90: 229-237.

Hettler, W.F. Jr. & Chester, A.J. 1990. Temporal distribution of ichthyoplankton near Beaufort Inlet, North Carolina. Marine Ecology - Progress Series 68: 157-168.

Hoese, D.F. 1984. Gobioidei: relationships. In: Moser, H.G. (Ed.). Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists: 588-591.

Hoese, D.F. 1986. Gobiidae. In: Smith, M.M. & Heemstra, P.C. (Eds.). Smiths' sea fishes 6th edition. Springer Verlag, Berlin: 774-807.

Hoetje, P., Westinga, E., Kruijf, H. de 1977. The intrasponge fauna of the loggerhead or manjack sponge (Porifera: *Spheciospongia vesperia* (Lamarck) Marshall). Proceedings of the Association of Island Marine Laboratories of the Carribean 12: 15.

Hoffman, C.J. 1981. Associations between the arrow goby *Clevelandia ios* (Jordan & Gilbert) and the ghost shrimp *Calianassa californiensis* dana in natural and artificial burrows. Pacific Science 35: 211-216.

Hose, J.E., King, T.D. & Stephens, J.S. Jr. 1984. Effects of dechlorinated seawater on fish behavior. Marine Environmental Research 11: 67-76.

Houde, E.D. & Lovdal, J.A. 1984. Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. Estuarine, Coastal and Shelf Science 18: 403-419.

Huh, S.-H. & Kitting, C.L. 1985. Trophic relationships among concentrated populations in seagrass meadows. Journal of Experimental Marine Biology and Ecology 92: 29-43.

Hur, S.-B. & Yoo, J.-M. 1984. Distribution of fish eggs and larvae in the western waters of Korea. Bulletin of the Korean Fisheries Society 17: 536-542.

Iwata, K. 1988. Nitrogen metabolism in the mudskipper, *Periophthalmus cantonensis*: Changes in free amino acids and related compounds in various tissues under conditions of ammonia loading, with special reference to its high ammonia tolerance. Comparative Biochemistry and Physiology 91A: 499-508.

Iwata, K. & Kakuta, I.A. 1983. Tobihaze to chichibu no kanzo oyobi kinniku no gurutamin san dasshuiso koso no seikagaku-teki seishitsu no hikaku. Comparison of catalytic properties of glutamate dehydrogense from liver and muscle between amphibious *Periophthalmus cantonensis* and water-breathing gobid fishes *Tridentiger obscurus obscurus*. Nissuishi 49: 1903-1908.

Iwata, M. & Bern, H.A. 1985. Responses to salinity and the effect of prolactin on whole anomal transepithelial potential in the gobiid teleost, *Gillichthys mirabilis*. General and Comparative Endocrinology 60: 434-440.

Janekarn, V. & Boonruang, P. 1986. Composition and occurrence of fish larvae in mangrove areas along the east coast of Phuket Island, western peninsular, Thailand. Research Bulletin of the Phuket Marine Biology Centre 44: 1-22.

Jenkins, G.P. 1986. Composition, seasonality and distribution of ichtyoplankton in Port Phillip Bay. Australian Journal of Marine and Freshwater Research 37: 507-520.

Johnson, W.S. & Chase, V.C. 1982. A record of cleaning symbiosis involving *Gobiosoma* sp. and a large Caribbean octopus. Copeia 3: 712-714.

Johnson, W.S. & Ruben, P. 1988. Cleaning behavior of *Bodianus rufus*, *Thalassoma bifasciatum*, *Gobiosoma evelynae*, and *Periclimenes padersoni* along a depth gradient at Salt River Submarine Canyon, St. Croix. Environmental Biology of Fishes 23: 225-232.

Jude, D.J., Reider, R.H. & Smith, G.R. 1992. Establishment of Gobiidae in the Great Lakes Basin. Canadian Journal of Fisheries and Aquatic Sciences 49: 416-421.

Karplus, I. 1987. The association between gobiid fishes and burrowing alpheid shrimps. Oceanography and Marine Biology Annual Review 25: 507-562.

Kerstitch, A. 1984. Unpalatable cleaners (banded cleaner goby). Sea Front. 30: 180-182.

Kikuchi, T. & Yamashita, Y. 1992. Seasonal occurrence of Gobiid fish and their food habits in a small mud flat in Amakusa. Publications of Amakusa Marine Biology Laboratory 11: 73-93.

Kim, Y.U. 1984. The distribution of fish larvae in the Korea Strait. Bulletin of the Korean Fisheries Society 17: 230-243.

Kinzie, R.A. III. 1988. Habitat utilization by Hawaiian stream fishes with reference to community structure in oceanic island streams. Environmental Biology of Fishes 22: 179-192.

Kopylets, S.K. & Dukravets, G.M. 1981. Morphometricheskaya i biologicheskaya charakteristika bychka *Rhinogobius similis* Gill., slichajnogo vselentsa v bassejn reki Ili. Voprosy Ikhtiologii 21: 600-607.

Krylov, V.I. 1984. An estimate of the effect of the Caspian seal (*Pusa caspia*) on fish populations. Canadian Translations in Fisheries and Aquatic Sciences 5066: 1-17.

Kulikova, N.I. 1985. Vliyanie khorionicheskogo gonadotropina na rost i sozrevanie ootsitov bychka - kruglyaka *Neogobius melanostomus* (Pallas) (Gobiidae) Voprosy Ikhtiologii 25: 300-312.

Leis, J.M. & Goldman, B. 1987. Composition and distribution of larval fish assemblages in the Great Barrier Reef Lagoon, near Lizard Island, Australia. Australian Journal of Marine and Freshwater Research 38: 211-223.

Leithiser, R.M. 1981. Distribution and Seasonal Abundance of Larval Fishes in a Pristine Southern California Salt Marsh. In: Lasker, R. & Sherman, K. (Eds.). The early life history of fish: recent studies. Rapports et Procès-verbaux du Conseil International pour l'Exploration de la Mer 178: 174-175.

Little, M.C., Reay, P.J. & Grove, S.J. 1988. The fish community of an East African mangrove creek. Journal of Fish Biology 32: 729-747.

Lopez-Jamar, E., Iglesias, J. & Otero, J.J. 1984. Contribution of infauna and mussel-raft epifauna to demersal fish diets. Marine Ecology - Progress Series 15: 13-18.

Lorenz, C.A. & Assad, J.A. 1986. Urotensin II lowers cytoplasmatic free calcium concentration in goby enterocytes: Measurements using quin2. General and Comparative Endocrinology 64: 355-361.

Low, W.P., Lane, D.J.W. & Ip, Y.K. 1988. A comparative study of terrestrial adaptations of the gills in three mudskippers -*Periophthalmus chrysopsilos*, *Boleophthalmus boddaerti*, and *Periophthalmodon schlosseri*. Biological Bulletin 175: 434-438.

Luckhurst, B.E. & Powles, H. 1981. Ichthyoplankton of the Central Venezuelan coast: Composition, abundance and seasonality. Proceedings of the Association of Island Marine Laboratories of the Carribean 16: 6.

Lugli, M., Bobbio, L., Torricelli, P. & Gandolfi, G. 1992. Breeding ecology and male spawning success in two hill-stream populations of the freshwater goby, *Padogobius martensi*. Environmental Biology of Fishes 35: 37-48.

Maeda Martinez, A., Contreras, S. & Maravilla, O. 1982. Abundancia y diversidad de la ictiofauna en 3 areas de manglar de la Bahia de la Paz, Mexico. Trans. Cibcasio. 6: 138-151.

Magnhagen, C. 1988. Changes in foraging as a response to predation risk in two gobiid fish species, *Pomatoschistus minutus* and *Gobius niger*. Marine Ecology - Progress Series 49: 21-26.

Magnhagen, C. 1990. Reproduction under predation risk in the sand goby, *Pomatoschistus minutus*, and the black goby, *Gobius niger*: the effect of age and longevity. Behavioral Ecology and Sociobiology 26: 331-335.

Magnhagen, C. 1992. Alternative reproductive behaviour in the common goby, *Pomatoschistus microps*: an ontogenetic gradient? Animal Behaviour 44: 182-184.

Magnhagen, C. & Kvarnemo, L. 1989. Big is better: the importance of size for reproductive success in male *Pomatoschistus minutus* (Pallas) (Pisces, Gobiidae). Journal of Fish Biology 35: 755-763.

Magnhagen C. & Forsgren, E. 1991. Behavioural responses to different types of predators by sand goby *Pomatoschistus minutus*: an experimental study. Marine Ecology - Progress Series 70: 11-16.

Magnhagen, C. & Vestergaard, K. 1991. Risk taking in relation to reproductive investments and future reproductive opportunities: field experiments on nest-guarding common gobies, *Pomatoschistus microps*. Behavioral Ecology 2: 351-359.

Maldonado, M.M. de C., Uribe-Alcocer, M., Arreguin-Espinosa, J. & Catsro-Perez, A. 1985. Karyotypical studies on *Dormitator maculatus* Bloch and *Gobiomorus dormitor* Lacépède (Gobiidae: Perciformes). Cytologia 50: 663-669.

McKay, S.I. & Miller, P.J. 1991. Isozyme criteria in the testing of phyletic relationships between species of *Gobius* and related eastern Atlantic-Mediterranean genera (Teleostei: Gobiidae). Journal of Fish Biology 39 suppl. A: 291-299.

Mehner, T. 1992. Diet spectra of *Pomatoschistus microps* (Krøyer) and *Pomatoschistus minutus* (Pallas) (Teleostei, Gobiidae). Zoologischer Anzeiger 229: 13-20.

Mehta, R.H., Mehta, S. & Devi, K. 1990. Structure and shape of mouth in some gobioid fishes. Environment and Ecology 8: 668-671.

Mendez Vargas, M. de L. 1980. Distribucion y abundancia del ictioplancton de la Laguna de Alvarado, Veracruz, a lo largo de un ciclo anual. UNAM, Mexico D.F.: 1-89.

Mestermann, K.D. & Zander, C.D. 1984. Vergleichende osteologische Untersuchungen an *Pomatoschistus*-Arten (Gobioidei, Pisces). Zoologisches Jahrbuch für Anatomie 111: 501-542.

Mihursky, J.A., Setzler-Hamilton, E., Martin, F.D., Jones, P., Ripple, K., Beaven, M. & Drewry, G. 1981. Resource utilization by larval fish in the upper Potomac Estuary. Estuaries 4: 245.

Miller, P.J. 1979. Adaptiveness and implications of small size in teleosts. Symposia of the zoological Society 44: 263-306.

Miller, P.J. 1981. A new *Pomatoschistus* from the Mediterranean, and redescription of *P. tortonesei* Miller 1968. Senckenbergiana biologica 62: 5-19.

Miller, P.J. 1984. The tokology of gobioid fishes. In: Potts, G.W. & Wootton, R.J. (Eds.). Fish reproduction: strategies and tactics. Academic Press, London: 119-153.

Miller, P.J. 1986. Gobiidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. & Tortonese, E., (Eds.). Fishes of the North-eastern Atlantic and the Mediterranean, Vol. III. Paris, UNESCO: 1019-1085.

Miller, P.J. 1987. Affinities, origin and adaptive features of the Australian desert goby *Chlamydogobius eremius* (Zietz, 1896) (Teleostei, Gobiidae). Journal of Natural History 21: 687-705.

Miller, P.J. 1990. The endurance of endemism: the Mediterranean freshwater gobies and their prospects for survival. Journal of Fish Biology 37 (Suppl. A): 145-156.

Miller, P.J. 1992a. A new species of *Didogobius* (Teleostei: Gobiidae) from the Adriatic Sea. Journal of Natural History 26: 1413-1419.

Miller, P.J. 1992b. The sperm duct gland: a visceral synapomorphy for gobioid fishes. Copeia 1992: 253-256.

Mina, M.V. 1992. Problems of protection of fish faunas in the USSR. Netherlands Journal of Zoology 42: 200-213.

Mizuno, N. 1980. Recent trends in investigations of freshwater gobies in Japan. In: Mori, S. & Ikusima, I. (Eds.). Proceedings of the first workshop on the promotion of limnology in the developing countries: 25-31.

Moiseeva, E.B. 1985. Experimental identification of pituitary thyrotropic cells in the goby *Neogobius melanostomus*. Journal of Evolutionary Biochemestry and Physiology 21: 111-118.

Mok, H.K. 1981. Sound production in the naked goby, *Gobiosoma bosci* (Pisces, Gobiidae) - a preliminary study. In: Tavolga, W.N., Popper, A.N. & Fay, R.R. (Eds.). Hearing and sound communication in fishes. Springer Verlag: 447-456.

Monteiro, R.W. 1982. Estudo do ictioplancton da regiao de Cabo Frio e areas vizinhas. Atlantica 5: 81.

Morton, R.M., Beumer, J.P. & Pollock, B.R. 1988. Fishes of a subtropical Australian saltmarsh and their predation upon mosquitoes. Environmental Biology of Fishes 21 : 185-194.

Müller, A. 1988. Seasonal change of zooplankton in Kiel bay: 4. Ichthyoplankton. Kieler Meeresforschungen (Sonderheft) 6: 323-330.

Murdy, E.O. 1985. Osteology of *Istiogobius ornatus*. Bulletin of Marine Science 36: 124-138.

Murdy, E.O. 1988. A taxonomic revision and cladistic analysis of the oxudercine gobies (Gobiidae: Oxudercinae). Records of the Australian Museum Supplement 11: 1-93.

Naess, T., Naas, K.E. & Samuelsen, O.B. 1991. Toxicity of rotenone to some potential predators on marine fish larvae -- an experimental study. Aquacultural Engineering 10: 149-159.

Nash, R.D.M. & Gibson, R.N. 1982. Seasonal fluctuations and composition of two populations of small demersal fishes on the west coast of Scotland. Estuarine, Coastal and Shelf Science 15: 485-496.

Nashida, K., Tominaga, O., Miyajima, H. & Ito, M. 1984. Niigata-ken hokubu engan ni okeru teisei gyorui no gunshu kozo. 1. Hirame jakureigyo no nikkan setsujiryo no suitei. Bulletin of the Japan Sea Regional Fisheries Research Laboratory 34: 1-17.

Natarajan, G.M. & Rajulu, G.S. 1983. Bimodal oxygen uptake in the amphibious mud-skipper *Periophthalmus koelreuteri* (Pallas) (Gobiidae: Teleostei). Journal of Animal Morphology and Physiology 30: 177-180.

Nayak, K. & Khuda-Bukhsh, A.R. 1987. Chromosomes of two species of fishes *Apocryptes* (Gobiidae: Pisces). Environmental Ecology 5: 371-373.

Oertzen, J.-A. von, Wulf, D. & Brügmann, L. 1988. Ecotoxicological effects of two mercury compounds on *Neomysis integer* (Leach) and *Pomatoschistus microps* (Krøyer). Kieler Meeresforschungen 6: 414-423.

Ogura, M. & Kishi, Y. 1985. Reproductive period and occupation of empty beverage cans by males of the crab, *Hemigrapsus penicillatus* (de Haan). Japanese Journal of Ecology 35: 377-385.

Oliver, M.P. & Rubies, P. 1987. Resultados preliminares sobre distribucion vertical del ictioplancton recogido en la campana SNEC I (septiembre 1985). Collected Science Papers ICSEAF 14: 149-167.

O'Sullivan, G. 1984. Seasonal changes in the intertidal fish and crustacean populations of Aughinish Island in the Shannon estuary. Irish Fisheries Investigations (B mar.) 28: 1-15.

Ozouf-Costaz, C. & Foresti, F. 1992. Fish cytogenetics research: advances, applications and perspectives. Netherlands Journal of Zoology 42: 277-290.

Paxton, J.R. & Hoese, D.F. 1985. The Japanese sea bass, *Lateolabrax japonicus* (Pisces, Percichthidae), an apparent marine introduction into eastern Australia. Japanese Journal of Ichthyology 31: 369-372.

Pezold, F. 1984. Evidence for multiple sex chromosomes in the freshwater goby *Gobionellus shufeldti* (Pisces: Gobiidae). Copeia 1984: 235-238.

Pezold, F. & Grady, J.M. 1989. A morphological and allozymic analysis of species in the *Gobionellus oceanicus* complex (Pisces: Gobiidae). Bulletin of Marine Science 45: 648-663.

Pinchuk, V.P. 1991. Species groupings in the genus *Neogobius* (Perciformes). Voprosy Ikhtiologii 31: 380-393.

Pinchuk, V.I. & Savchuk, M.Y. 1982. Species composition of the genus *Pomatoschistus* (Gobiidae) in the seas of the USSR. Journal of Ichthyology 22: 7-12.

Potter, I.C., Beckley, L.E., Whitfield, A.K. & Lenanton, R.J.C. 1990. Comparisons between the roles played by estuaries in the life cycle of fishes in temperate Western Australia and Southern Africa. Environmental Biology of Fishes 28: 143-178.

Powell, A.B., Hoss, D.E., Hettler, W.F., Peter, D.S. & Wagner, S. 1989. Abundance and distribution of ichthyoplankton in Florida Bay and adjacent waters. Bulletin of Marine Science 44: 35-48.

Provancha, M.J. & Hall, C.R. (1991). Ecology and life history of the clown goby inhabiting the upper Banana River, Cape Canaveral, Florida. Environmental Biology of Fishes 31: 41-54.

Rab, P. 1985. Karyotype of the Danube goby, *Proterothinus marmoratus* (Pisces, Gobiidae). Folia Zoologica Brno 34: 329-334.

Radtke, R.L., Kinzie, R.A. III & Folsom, S.D. 1988. Age and recruitment of Hawaiian freshwater gobies. Environmental Biology of Fishes 23: 205-213.

Ramos-Porto, M. & Vasconcelos, A.F.L. de 1980. Estudo da disponibilidade de alimentos para os peixes centropomideos da regiao de Itamaraca (Pernambuco-Brasil) 1. Simposio Brazileiro de aquicultura: 185-192.

Rengarajan, K. & Raj, J.D. 1985. On the ichthyoplankton of Cochin Backwater during spring tide. Symposium series of the Marine Biology Association of India 6: 998.

Robert, F., Renaud, F., Mathieu, E. & Gabrion, C. 1988. Importance of the paratenic host in the biology of *Botriocephalus gregarius* (Cestoda, Pseudophyllidea), a parasite of the turbot. International Journal of Parasitology 18: 611-621.

Robertson, D.R. & Justines, G. 1982. Protogynous hermaphroditism and gonochorism in four Caribbean reef gobies. Environmental Biology of Fishes 7: 137-142.

Rogers, S.I. 1988. Reproductive effort and efficiency in the female common goby, *Pomatoschistus microps* (Krøyer)(Teleostei: Gobioidei). Journal of Fish Biology 33: 109-119.

Rojo, A.L. 1985. Osteologia del chanquete, *Aphya minuta* (Risso, 1810) (Pisces: Gobiidae). Boletin del Instituto Español de Oceanografia 2: 165-179.

Rouse, G.W. & Pickles, J.O. 1991. Ultrastructure of free neuromastts of *Bathygobius fuscus* (Gobiidae) and canal neuromasts of *Apogon cyanosoma* (Apogonidae). Journal of Morphology 209: 111-120.

Ryan, P.A. 1991. The success of the Gobiidae in tropical Pacific insular streams. New Zealand Journal of Zoology 18: 25-30.

Sakai, M. & Goto, A. 1982. Studies on the freshwater fish in Hokkaido, Japan - I. Breeding habits, growth and distribution of a goby, *Chaenogobius castanea* (O'Shaughnessy). Bulletin faculty of Fisheries of the Hokkaido University 33: 9-23.

Salvanes, A.G.V., Aksnes, D.L. & Giske, J. 1992. Ecosystem model for evaluating potential cod production in a west Norwegian fjord. Marine Ecology - Progress Series 90: 9-22.

Setzler-Hamilton, E.M. 1987. Utilization of Chesapeake Bay by early life history stages of fishes. In: Majumdar, S.K., Hall, L.W. Jr & Austin, H.M. (Eds.). Contaminant problems and management of living Chesapeake Bay resources: 63-93.

Sievers, U. 1989. Nahrungsökologische Untersuchungen an Seehunden (Phoca vitulina, Linné 1758) aus dem Schleswig-holsteinischen Wattensee. Zoologischer Anzeiger 222: 449-460.

Smith, R.J.F. 1989. The response of *Asterropteryx semipunctatus* and *Gnatholepis anjerensis* (Pisces, Gobiidae) to chemical stimuli from injured conspecifics, an alarm response in gobies. Ethology 81: 279-290.

Smith, R.J.F & Smith, M.J. 1989. Predator-recognition behaviour in two species of gobiid fishes, *Asterropteryx semipunctatus* and *Gnatholepis anjerensis*. Ethology 83: 19-30.

Smith, R.J.F., Lawrence, B.J. & Smith, M.J. 1991. Cross-reaction to skin extract between two gobies, *Asterropteryx semipunctatus* and *Brachygobius sabanus*. Journal of Chemical Ecology 17: 2253-2260.

Sokolov, L.I., Tsepkin, E.A., Sokolova, E.L. & Golovatyuk, G.Y. 1989. Novye zhiteli Moskvy-reki. (New inhabitants of the Moskva River). Priroda 9: 80-81.

Sponder, D.L. & Lauder, G.V. 1981. Terrestrial feeding in the mudskipper *Periophthalmus* (Pisces: Teleostei): a cineradiographic analysis. Journal of Zoology 193: 517-530.

Springer, V.G. 1983. *Tyson belos*, new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of Gobioid osteology and classification. Smithsonian Contributions to Zoology 390: 1-40.

Sunobe, T. & Nakazono, A. 1987. Embryonic development and larvae of the genus *Eviota* (Pisces: Gobiidae). I. *Eviota abax* and *E. storthynx*. Journal of the Faculty of Agriculture, Kyushu University 31: 287-295.

Sunobe, T. & Nakazono, A. 1990. Polygynous mating system of *Trimma okinawae* (Pisces: Gobiidae) at Kagoshima, Japan with a note on sex change. Ethology 84: 133-143.

Takami, A., Etessami, G.H. & Saremi, S. 1980. Régime alimentaire des esturgeons (Acipenserides) sur les côtes sud de la Mer Caspienne. Cybium 10: 65-72.

Thode, G., Cano, J. & Alvarez, M.C. 1983. A karyological study on four species of Mediterranean gobiid fish. Cytologia 48: 131-138.

Thode, G., Martinez, G., Ruiz, J.L. & Lopez, J.R. 1988. A complex chromosomal polymorphism in *Gobius fallax* (Gobiidae, Perciformes). Genetica 76: 65-71.

Thorman, S. & Wiederholm, A.-M. 1986. Food, habitat and time niches in a coastal fish species assemblage in a brackish water bay in the Bothnian Sea, Sweden. Journal of Experimental Marine Biology and Ecology 95: 67-86.

Torricelli, P., Lugli, M., Gandolfi, G. 1985. A quantitative analysis of the fanning activity in the male *Padogobius martensi* (Pisces: Gobiidae). Behaviour 92: 289-301.

Torricelli, P., Lugli, M., Gandolfi, G. 1986. A quantitative analysis of the occurrence of visual and acoustic displays during the courtship in the freshwater goby, *Padogobius martensi* (Guenther, 1961) (Pisces, Gobiidae). Bollettino di Zoologia 53: 85-89.

Tyler, J.C. & Böhlke, J.E. 1972. Records of sponge-dwelling fishes, primarily of the Caribbean. Bulletin of Marine Science 22: 601-642.

Utne, A.C.W., Aksnes, D.L. & Giske, J. 1993. Food, predation and shelter: an experimental study on the distribution of adult two-spotted goby *Gobiusculus flavescens* (Fabricius). Journal of Experimental Marine Biology and Ecology 166: 203-216.

Vitturi, R. & Catalano, E. 1989. Multiple chromosome polymorphism in the gobiid fish *Gobius niger jozo* L. 1758. (Pisces, Gobiidae). Cytologia 54: 231-235.

Voris, H.K. & Voris, H.H. 1983. Feeding strategies in marine snakes: An analysis of evolutionary, morphological, behavioural and ecological relationships. American Zoologist 23: 411-425.

Wallis, G.P. & Beardmore, J.A. 1984. An electrophoretic study of the systematic relationships of some closely related goby species (Pisces, Gobiidae). Biological Journal of the Linnean Society 22: 545-567.

Warnock, N. 1989. Piracy by ring-billed gulls on dunlin. Wilson Bulletin 101: 96-97.

Webb, C.J. 1980. Systematics of the *Pomatoschistus minutus* complex (Teleostei: Gobiidae). Philosophical Transactions of the Royal Society (B) 291: 201-241.

Webb, C.J. 1986. Karyology of *Pomatoschistus microps* (Teleostei: Gobioidei). Journal of the marine biological Association of the United Kingdom 66: 259-266.

Whitfield, A.K. 1989. Ichthyoplankton in a southern African surf zone: Nursery area for the postlarvae of estuarine associated fish species? Estuarine, Coastal and Shelf Science 29: 533-547.

Wickstroem, H. & Enderlein, O. 1991. The significance of by-catches of other fish than eels in eel traps. In: Nyman, L. (Ed.). Inland fisheries research in Sri Lanka: contributions by staff of the National Swedish Board of Fisheries. Fisheries Development Series of the National Swedish Board of Fisheries 50: 27-37.

Wilkins, H.K.A. & Myers, A.A. 1992. Microhabitat utilisation by an assemblage of temperate Gobiidae (Pisces: Teleostei). Marine Ecology - Progress Series 90: 103-112.

Williams, E.H. Jr. & Williams, L.B. 1986. The first association of an adult mollusk (Nudibranchia: Doridae) and a fish (Perciformes: Gobiidae). Venus Japanese Journal of Malacology 45: 10-211.

Winterbottom, R. 1990. The *Trimmatom nanus* species complex (Actinopterygii, Gobiidae): Phylogeny and progenetic heterochrony. Systematic Zoology 39: 253-265.

Winterbottom, R. & Emery, A.R. 1986. Review of the gobioid fishes of the Chagos Archipelago, Central Indian Ocean. Royal Ontario Museum. Life Sciences Contributions 142: 1-82.

Wright, J.M. 1986. The ecology of fish occurring in shallow water creeks of a Nigerian mangrove swamp. Journal of Fish Biology 29: 431-441.

Wyanski, D.M. & Targett, T.E. 1985. Juvenile development of the Lyre goby, *Evorthodus lyricus* (Girard) (Pisces: Gobiidae), with a discussion of early life history. Bulletin of Marine Science 36: 115-123.

Yadav, A.N., Prasad, M.S. & Singh, B.R. 1990. Gross structure of the respiratory organs and dimensions of the gill in the mud-skipper, *Periopthalmodon schlosseri* (Bleeker). Journal of Fish Biology 37: 383-392.

Yamaoko, K., Hori, M. & Kuratani, S. 1986. Ecomorphology of feeding in 'goby-like' cichlid fishes in Lake Tanganyika. Physiological Ecology Japan 23: 17-29.

Yamaoko, K., Takagi, M. Yamada, T. & Taniguchi, N. 1991. Territorial behaviour of released juvenile red sea bream. Nippon Suizan Gakkaishi 57: 1-5.

Yazdandoust, M.H. 1985. Cancer crab larvae and goby fish: Vector and victim of paralytic shellfish poisons (PSP). In: Anderson, D.M., White, A.W. & Banden, D.G. (Eds.). Toxic dinoflagellates. St-Andrews, Canada : 419-424.

Yoo, J.M. & Cha, S.S. 1988. Variation of abundances of icthyoplankton in Kwangyang Bay. Oceanic Research 10 : 79-84.

Zander, C.D. & Döring, W. 1989. The role of gobies (Gobiidae, teleostei) in the food web of shallow habitats of the Baltic Sea. Proceedings 21st European Marine Biology Symposium: 499-508.

Zerunian, S. & Gandolfi, G. 1986. Considerazioni sui gobidi d'acqua dolce presenti nel basso Lazio (Pisces, Gobiidae). Rivista di Idrobiologia 25: 69-80.

Zhiqing, F. & Ronqing, T. 1987. Xiahuyu yamu sizhongyu de ranseti zuxing de chubu yanjiu. Studies on the karyotypes of four species in Gobioide and compared with other fishes in there. Zhejiang Shuichan Xueyuan Xuebao (Journal of the Zhejiang College of Fisheries) 6: 127-131.

Chapter 2

The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands): Spatial structure.

Hamerlynck, O., Hostens, K., Arellano, R.V., Mees, J. & Damme, P.A. van (in press). The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands): Spatial structure. Netherlands Journal of Aquatic Sciences.

ABSTRACT

During 1989 monthly beam trawl samples were collected at 48 stations in the Dutch Delta. The annual mean densities of the demersal fishes and mobile epibenthic invertebrates at these stations were calculated. These data were then subjected to multivariate statistical techniques for an analysis of the spatial structure of the communities found and to study the relationship between these communities and their environment.

The present study confirms the results of Henderson (1989) in that, given a fairly limited number of environmental variables, mainly salinity and exposure/substratum type, quite accurate predictions of the type of community expected at a certain site can be made. The explicit inclusion of epibenthic invertebrates, a dominant group in most assemblages, in studies mainly targeted at demersal fishes, is strongly recommended.

In the Dutch Delta rich and varied communities exist in the Voordelta. A number of groups, such as salmonids, anadromous species and starfish, expected in the Westerschelde are absent or extremely rare probably as a consequence of pollution stress. The Oosterschelde is relatively poor in density terms but has a highly diverse epibenthic fauna dominated by fishes.

INTRODUCTION

Most studies reporting on fishes and larger epibenthic invertebrates (e.g. shrimps, crabs) are heavily biased towards the exploited life stages of commercial species. Despite general agreement on the qualitative notion that estuaries and shallow coastal areas are important nurseries for marine fishes (Haedrich 1983) there is still a need for quantitative studies. In comparison to macrobenthic studies there are relatively few studies describing the structure of estuarine fish communities and these have been mainly restricted to British estuaries (Claridge *et al.* 1986, Henderson 1989, Elliott *et al.* 1990). Some comparative exercises have been done (Costa & Elliott 1991, Pomfret *et al.* 1991) and functional studies are beginning to emerge (Elliott & Taylor 1989, Hostens & Hamerlynck in press). Process studies have as yet been restricted to single species of commercial importance (e.g. Veer 1986).

The development of multivariate statistical techniques has created the possibility of summarising the structure in large multispecies data sets. These techniques are very popular in many ecological fields (review in James & McMulloch 1990) but have rarely been used in studies of marine fishes of the North Sea. Henderson (1989) used Principle Component Analysis to analyse the structure of the fish communities as recorded from the intake screens of power stations in England and Wales. Daan *et al.* (1990) applied an unspecified type of cluster analysis to the fifty most abundant fish species recorded in the English Groundfish Surveys 1982-1985. Though the sampling gears deployed to sample fish catch a number of mobile epibenthic invertebrates, these animals are rarely integrated into the results.

In this study a multivariate analysis of the spatial structure of the mobile epifauna of the Dutch Delta, on the basis of annual mean density and biomass, is presented. The study is restricted to soft bottoms. An attempt is made to assess the correlation between the occurrence of a certain species assemblage and its environment. A lot of detail is provided on the practical strategy for the multivariate analysis. These details are not often reported in papers but may be important to judge if the choice of the technique and the way in which it was applied were adequate (James & McCulloch 1990).

The purpose of this study is to provide a baseline for future functional and process studies of the mobile epifauna of the Delta area and of the Westerschelde in particular. These will have to be based on spatial units coinciding with the biological communities. To comply with international standards a massive reduction of the pollution load of the Westerschelde will have to be achieved in the (near?) future and the impact assessment of these changes will hopefully be monitored. A baseline study is a prerequisite for such a monitoring programme.

MATERIALS AND METHODS

Study area (Fig. 2.1)

Three main European rivers: the Rhine, Meuse and Schelde, enter the North Sea in the Dutch Delta region in the south-western part of the Netherlands. Most of the former estuaries in this area have been altered by man (review in Heip 1989). The study area covers only three parts of the Dutch Delta: the Westerschelde, the Oosterschelde and the central part of the Voordelta.

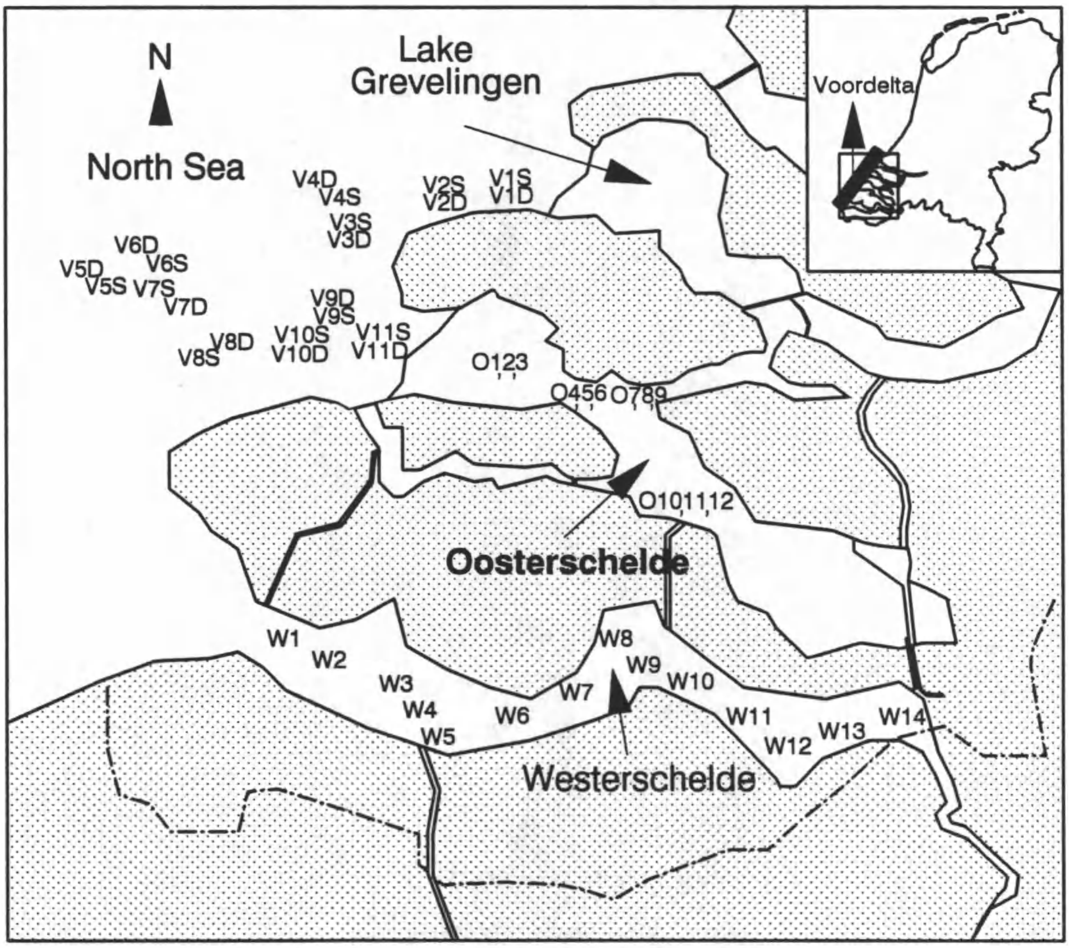


Fig. 2.1. Map of the study area with the sampling stations.

The lower part of the river Schelde is generally known as the Westerschelde estuary. It is the last remaining true estuary in the Dutch Delta and exhibits marked gradients in salinity, oxygen and turbidity. The mean fresh water load is 105 m^3 s^{-1} (Herman *et al.* 1991). The input of organic and inorganic pollutants is very high, especially in the brackish part (Duursma *et al.* 1988, Eck *et al.* 1991). The division between the marine and the brackish part is situated between stations W8 and W9 (Fig. 2.1) (Hummel *et al.* 1988).

The former Oosterschelde estuary is now a tidal inlet of the Southern Bight of the North Sea. By the construction of a number of dams in the landward part, the fresh water inflow was reduced to 55 m^3 s^{-1} and in 1986 a storm surge barrier was completed at the mouth. This caused substantial changes in the functional characteristics of the ecosystem (Bakker *et al.* 1990). Some impact could also be detected on the fishes and epibenthic invertebrates (Hamerlynck & Hostens in press, Hostens & Hamerlynck in press).

The Voordelta is the shallow coastal area formed by the interlinked ebb tidal deltas of the (former) estuaries of the Dutch Delta. It extends from the Belgian-Dutch border in the South to the Hoek van Holland in the North. Its marine boundary is arbitrarily defined by the Mean Tidal Level (MTL) -10 m isobath. The closure of the former estuaries has had an important impact on the geomorphology (Louters *et al.* 1991) and ecology (Hamerlynck *et al.* 1992) of the area. Only the central part of the Voordelta: the ebb tidal delta of the former Grevelingen estuary and the ebb tidal delta of the Oosterschelde, have been investigated in this study.

Sampling

During 1989 monthly samples were taken at twenty-two stations in the Voordelta, twelve stations in the Oosterschelde, and fourteen stations in the Westerschelde (Fig. 2.1). In the Voordelta the twenty-two stations cover two depth strata (MTL - 5m and MTL -10m) at eleven localities. In the Oosterschelde the twelve stations correspond to three parallel tows at four localities. In the Westerschelde the stations are located at the edges of the ebb-tidal channel from the mouth to the Belgian-Dutch border. Several trials were made to sample further upstream but, due to the inordinate amount of rubbish covering these grounds, gear loss was so frequent that no results can be reported (see also Pomfret *et al.* 1991).

In January and August the six most seaward stations of the Voordelta could not be sampled because of adverse weather conditions. Five other Voordelta samples and 5 Westerschelde samples were lost because the net was torn or the beam trawl hit an obstacle.

Samples were taken from the R.V. Luctor (34 m, 500 Hp) using a 3 metre beam trawl, equipped with a 6 metre long net with a 5*5 mm mesh in the cod end, a tickler chain and a chain in the groundrope. Hauls were 1 km in length. Ship speed relative to the bottom when trawling is on average 4.5 knots. All fishes, with the exception of the gobies, were identified to species level on board. Gobies of the genus *Pomatoschistus* were preserved for identification in the laboratory (Hamerlynck 1990). As the invertebrates were treated more or less in bulk, a number of rare species were overlooked: the shrimps *Crangon allmani*, *Pontophilus trispinosus*, *Processa modica modica* and *Pandalus montagui*, the crabs *Portumnus latipes*, *Liocarcinus arcuatus* and *Macropodia rostrata*. Specimens of these species were occasionally observed in the Voordelta but were not quantified. *C. allmani*, *P. montagui* and the three crab species mentioned were also sometimes noted in the Oosterschelde catches. In the Westerschelde *Palaemonetes varians* was seen occasionally. The hermit crab *Pagurus bernhardus* is a common occurrence but was not quantified. Cephalopoda and Echinodermata Crinoidea were also sometimes caught but not quantified.

Standard length was recorded for all fish specimens. Biomass was calculated from length - Ashfree Dry Weight (ADW) regressions compiled for the Dutch Delta by K. Hostens (unpubl. data). Invertebrates were counted and (wet)weighed. Net efficiency was assumed to be 20 % for all size classes of fish and invertebrates. This assumption is based on the work of Kuipers (1975) on plaice. For the relatively immobile starfish efficiency was assumed to be 40 %. Efficiency adjusted densities are given as N per 1000 m^2, biomass as g ADW per 1000 m^2.

Environmental variables

At each site the following environmental variables were measured during the sampling: salinity (ppt), water temperature (°C), water depth (m), Secchi disk depth (m) and oxygen content (mg l^{-1}). Salinity, temperature and oxygen content were measured at about 1 m above the bottom. For these variables means were calculated per station. These averages are not true annual means because they were only calculated for those months in which all stations were sampled. The measurements in January and August were therefore not included in the calculations. In November no measurements could be taken because of a technical failure of the probe.

In December 1988 hyperbenthos samples were taken with a hyperbenthic sledge at all the stations according to the methodology described in Mees &

Hamerlynck (1992). The hyperbenthic biomass data (mg ADW m^{-2}) were taken from that study. At each sampling station of the Westerschelde and Oosterschelde three Van Veen grabs were taken and sieved over a 1-mm mesh. Macrobenthic biomass (g ADW m^{-2}), mud content (%) and median grain size of the sand fraction (μm) were measured. Macrobenthic biomass data for the Voordelta stations were taken from Craeymeersch *et al.* (1990). The sediment composition data for the Voordelta and the 1% wave height (the wave height exceeded for 1% of the year) were taken from Dijke & Buijs (1987).

Benthic biomass data were collected to investigate possible correlations between epifauna and their main food. Wave height is used as a measure of exposure.

Table 2.1. Ranges of the environmental variables measured with (between brackets) the station at which the extremes were recorded, the mean for all stations and the standard deviation (SD) of that mean.

VARIABLE (unit)	MINIMUM	MAXIMUM	MEAN	SD
Salinity (ppt)	13.4 (W14)	32.1 (V7)	28.5	5.0
Temperature (°C)	11.5 (V2)	13.2 (W14)	12.0	0.4
Depth (m)	5.3 (V1S)	21.7 (OR2)	10.4	3.7
Secchi depth (m)	0.5 (W14)	3.3 (OW)	1.9	0.9
Oxygen (mg l^{-1})	7.4 (W14)	10.6 (V2)	10.0	0.5
Hyperbenthos (mg ADW m^{-2})	0.02 (OW)	242 (W14)	19.4	56
Macrobenthos (g ADW m^{-2})	0 (W12-W14)	90 (V1D)	7.2	18
Mud content (%)	0 (V4D,W6,W11)	20 (V1D)	2.8	3.7
Median grain size (μm)	125 (V1D)	357 (W3)	230	56
1% significant wave (m)	1 (OW,W11-W14)	3.5 (V5)	1.8	0.7

Table 2.1 summarises the range of the environmental variables recorded. It should be noted that only the means per station are shown and that in some months more extreme values have been recorded, e.g. 4 mg l^{-1} of oxygen in April in station W14.

Multivariate analysis of community structure

Density and biomass data from each haul were subjected to a fourth root transformation prior to further analysis (Clarke & Green 1988). This partly compensates for the deviation from normality typical for species abundance data. The transformed data set then still contains an inordinate amount of zero observations. Eliminating rare species (Field *et al.* 1982, Henderson 1989, Daan *et al.* 1990) may alleviate this, but it entails a loss of information. In the present, relatively species-poor data set, no *a priori* reduction of the number of species was accomplished.

All hauls at a sampling station were considered to be replicates and the annual means of (the transformed) density and biomass were calculated.

The data were subjected to a Two Way Indicator Species Analysis (TWINSPAN, Hill 1979) and a Group Average Sorting (GAS) using the Bray-Curtis similarities (Bray & Curtis 1957). The clusters of stations distinguished by both techniques were then compared. The choice of the cut levels in the TWINSPAN was based on a simple rule of thumb: the number of observations (e.g. density values) within each cut level should be approximately equal, except for the lowest cut level which contains all the zero observations and the two highest cut levels which contain approximately half as many observations as the other levels. In this way some extra weight was given to the commonest species. Cut levels chosen for the density data were: 0 0.11 0.2 0.4 0.7 1.2 2.1 and 3. For the biomass data these were 0 0.15 0.36 0.81 1.59 2.3 and 4.2. All other settings in the TWINSPAN are default, with the exception of the maximum number of divisions which was set to four instead of six.

The data were then subjected to ordination techniques from the CANOCO package (Braak 1988). A Correspondence Analysis (CA) was done to assess total community variability and to compare the scales of the species scores and the sample scores (Jongman *et al.* 1987, Braak & Prentice 1988). Next, a Principal Component Analysis (PCA) was performed, combining the biotic data with the environmental variables.

In the PCA euclidean distances were calculated from the correlation matrix

(James & McCulloch 1990). Environmental variables were centred, i.e. replaced by the deviation from the mean for all stations (Jongman *et al.* 1987). As the underlying response model of PCA is linear, the hyperbolic relationship which was found between Secchi disk depth and the first ordination axis was linearised by a reciprocal transformation of this variable.

When characterising a community, Hill's diversity numbers (Hill 1973) of the order 0, 1, 2 and $+\infty$ are of particular interest (Heip *et al.* 1988). For each of these Hill numbers the means and standard deviations were calculated per assemblage. With increasing order of the Hill number, the influence of dominant species increases and the influence of species richness decreases (see also Mees *et al.* in press b).

Terminology

All Voordelta samples were taken in inshore waters but to simplify the description of the results the most seaward stations (V5 to V7) are labelled 'offshore' stations in comparison to the stations V1 to V3 and V9 to V11 that are labelled 'inshore'. The V4 and V8 stations are labelled 'intermediate'. The word 'locality' refers to a broader site including two stations in the Voordelta (e.g. locality V1 is composed of stations V1S and V1D) and three stations in the Oosterschelde. In the figures species names were shortened to eight letters: the first four letters of the genus and the first four of the species name.

RESULTS

Species composition

A total of 53 species were quantified (Table 2.2). These species are classified into six ecological types according to the use they make of estuarine areas (Elliott & Taylor 1989, Costa & Elliott 1991). Eighteen species are truly marine and do not depend on estuaries for any part of their life-cycle (MO in Table 2.2), sixteen species are estuarine resident species (ER), ten marine species make use of the estuary as a nursery ground (MJ), five species are catadromous or anadromous (CA), three marine species spend part of the year in the estuarine environment as adults (MS). The three-spined stickleback *Gasterosteus aculeatus* is difficult to classify. It is partly a freshwater species, partly estuarine resident (FW/ER).

Table 2.2. List of the species quantified with their abundance (N per 1000 m^2) in the different assemblages and their ecological type (see text for explanation).

	Assemblage							
Species name	VX	VIO	VIG	OI	OO	WM	WB	
Lampetra fluviatilis						<0.1		CA
Anguilla anguilla	<0.1	0.5	0.1	0.1	0.9	0.3	0.6	CA
Clupea harengus	11	20	62	3	10	3	6	MJ
Sprattus sprattus	22	7	29	18	3	24	18	MJ
Alosa fallax							0.1	CA
Engraulis encrasicolus	<0.1		<0.1	<0.1	0.1	0.1	0.1	ER
Gadus morhua	0.2	1	1		0.2	0.2	0.2	MJ
Merlangius merlangus	3	23	54	2	7	3	<0.1	MJ
Trisopterus luscus	0.8	7	10	7	11	1	2	MJ
Trisopterus minutus				<0.1	0.1			MO
Ciliata mustela	<0.1	0.4	2	0.1	0.1	0.2	0.6	MS
Zoarces viviparus	<0.1		0.3	3	0.6		0.2	ER
Atherina presbyter	0.1	0.7	0.6	1	0.1	<0.1	<0.1	ER
Gasterosteus aculeatus	0.2				0.3		0.3	FW/ER
Syngnathus acus	0.1		0.1	0.4	0.1	<0.1		ER
Syngnathus rostellatus	4	6	12	15	3	4	7	ER
Entelurus aequoreus	<0.1		<0.1	0.1	<0.1			MO
Trigla lucerna	0.3	0.4	0.8	0.4	0.1	0.1	<0.1	MJ
Myoxocephalus scorpius	0.1	1	0.5	1	0.2	0.1	0.3	ER
Taurulus bubalis				0.1	<0.1			MO
Agonus cataphractus	0.2	4	9	0.8	0.1	0.3	0.4	ER
Liparis liparis	0.1	2	1		<0.1	0.7	0.6	ER
Dicentrarchus labrax		0.1		<0.1			0.1	MJ
Trachurus trachurus	<0.1			3	0.4	<0.1		MO
Mullus surmuletus	0.3	0.6	0.3	<0.1				MO
Mugilidae species			0.5	0.1	0.2	0.1	0.1	CA
Trachinus vipera	0.2							MO
Pholis gunnellus			0.6	0.4	<0.1			ER
Ammodytes tobianus	26	0.7	2	0.1	0.5	4	2	ER
Hyperoplus lanceolatus	2		0.1			0.7	<0.1	MO
Callionymus lyra	10	42	25	15	0.7			MO
Pomatoschistus microps	<0.1			0.7	0.3	3	3	ER
Pomatoschistus pictus	4	4	5	0.3	0.2	<0.1		MO
Pomatoschistus minutus	50	64	506	161	37	39	118	MS
Pomatoschistus lozanoi	105	38	221	3	2	143	192	MS
Aphia minuta	0.2	1	2		0.1			MO
Gobius niger				<0.1				ER
Scophthalmus rhombus	0.1		0.1	0.2	0.2	<0.1		MO
Scophthalmus maximus	0.1		0.1					MO
Pleuronectes platessa	3	48	19	63	25	3	13	MJ
Limanda limanda	14	67	133	43	8	11	44	MJ
Pleuronectes flesus	0.1	1	2	0.2	<0.1	0.4	5	CA
Solea solea	0.2	12	9	2	0.7	4	8	MJ
Buglossidium luteum		0.1	0.2					MO
Microstomus kitt				0.3				MO
Arnoglossus laterna	<0.1							MO
Crangon crangon	697	1224	3071	446	460	1358	2467	ER
Liocarcinus holsatus	44	122	572	16	10	9	2	MO
Carcinus maenas	1	15	42	73	7	21	12	ER
Cancer pagurus	0.1	0.9			0.1			MO
Eriocheir sinensis							<0.1	ER
Homarus gammarus				<0.1				MO
Asterias rubens	175	1226	5426	106	132			ER

Spatial structure

The results of the analyses with the biomass data were very similar to those of the corresponding analyses using the density data. Therefore, except for the TWINSPAN, only the density results are reported.

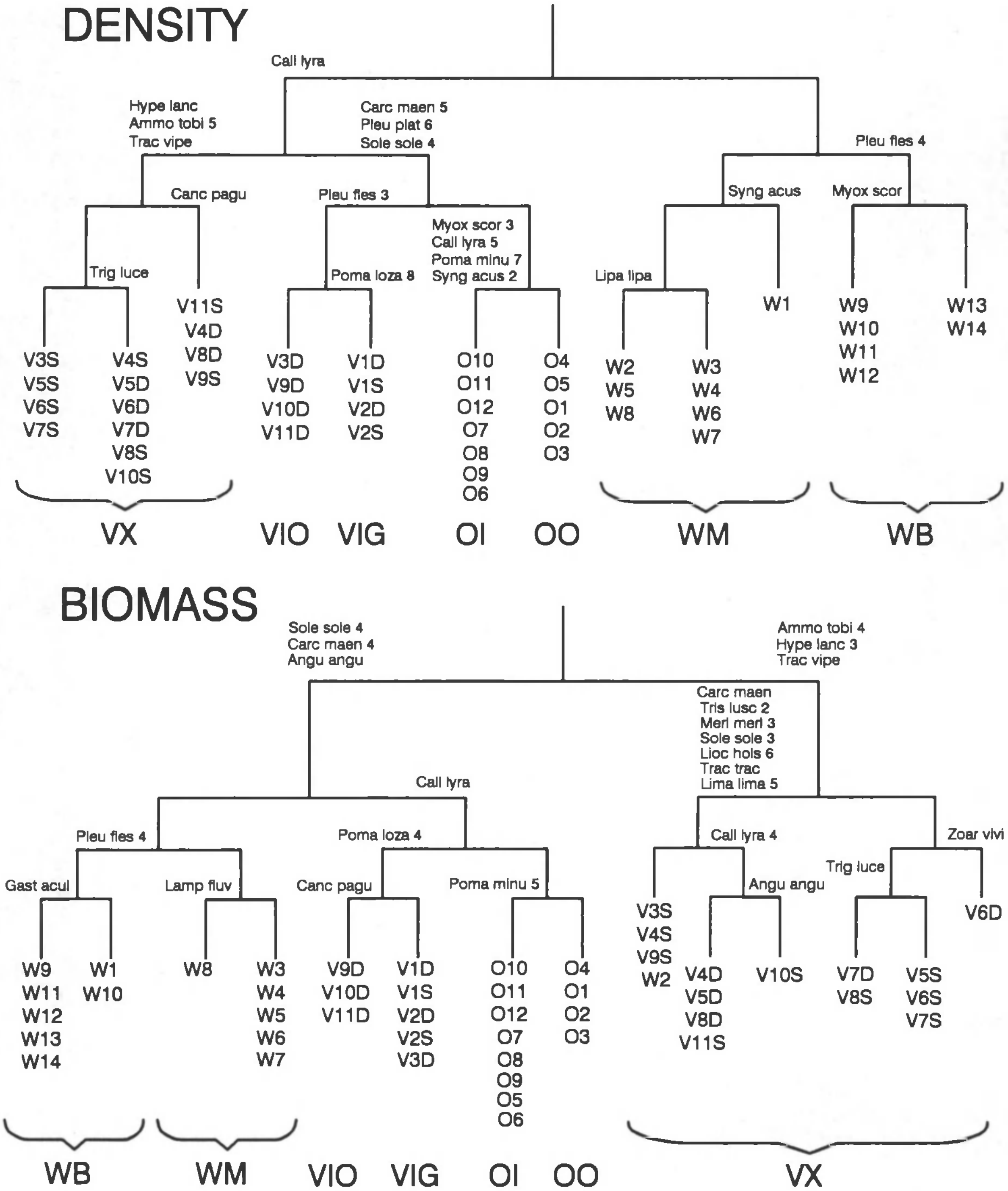


Fig. 2.2. Results of the TWINSPAN for density (top) and biomass (bottom). Indicator species are indicated with their cut level (level 1 is not indicated).

Classification

The result of the TWINSPAN (first division eigenvalue 0.13) using the density data is shown in Fig. 2.2 (top). The first division separates the Westerschelde stations from the rest. Within this last group the next division separates a cluster, mainly composed of offshore and intermediate Voordelta stations (VX).

In the Westerschelde cluster the next division splits the stations in the brackish part (WB) from the stations in the marine part (WM).

Further divisions in the central cluster first separate the Oosterschelde stations from the inshore Voordelta and then split each of these into two smaller groupings. Thus four clusters are created, grouping
- the deep inshore stations in the ebb tidal delta of the Oosterschelde (VIO)
- the inshore stations in the ebb tidal delta of the Grevelingen (VIG)
- the stations in the most landward part of the Oosterschelde (OI)
- the more seaward stations of the Oosterschelde (OO).

The TWINSPAN result (first division eigenvalue 0.14) for the biomass data (Fig. 2.2, bottom) resembles the result for the density data, though the order in which the groupings are separated and the indicator species may differ. Some stations are in a different cluster when comparing both results. Station W1, in the mouth of the Westerschelde is found in the WB cluster of the biomass result. Station V3D from the ebb tidal delta of the Grevelingen is classified into the VIO cluster in the density result.

In the GAS the same four major clusters can be recognized as separate entities (Fig. 2.3): the WS cluster, the OS cluster, the VI cluster (this time without V10D) and the VX cluster. Within the WS cluster the WB cluster lacks the stations W9 and W12. In the VX cluster (which now includes V10D) there is a subcluster grouping the shallow offshore stations and V8S. In the OS cluster the three stations from each of the four localities form tight clusters. In the VI cluster the VIG stations are found in close association. Station V3D is again closely associated to the VIO stations V9D and V11D.

Characterisation of the species assemblages

From the results of the classification techniques it is clear that seven different clusters of stations can be defined: two in the Westerschelde (WM and WB), two in the Oosterschelde (OW and OE) and three in the Voordelta (VX, VIG and VIO).

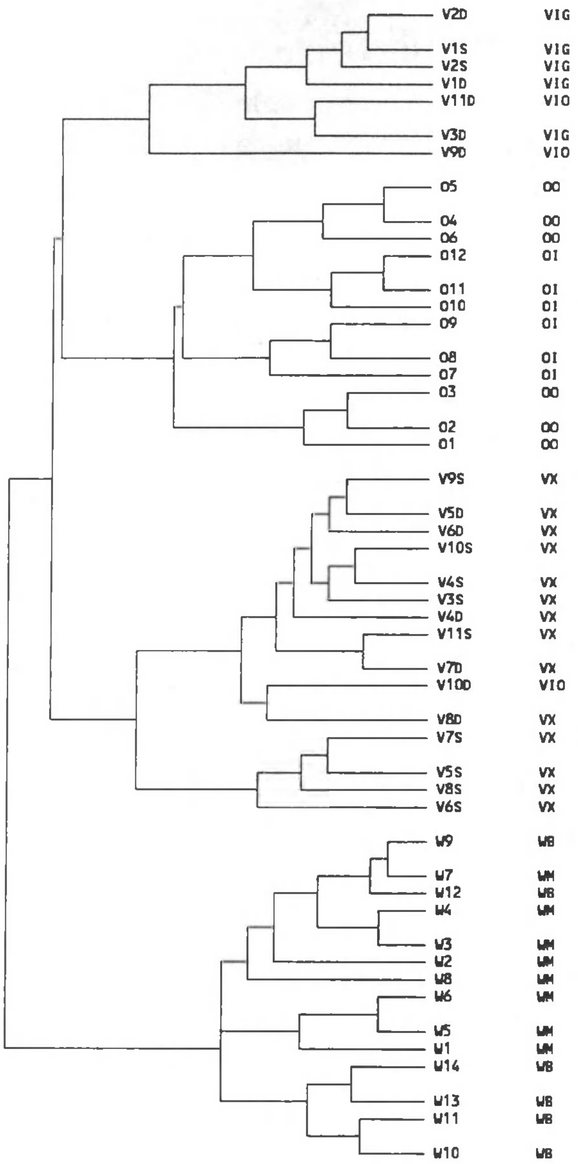


Fig. 2.3. Results of the Group Average Sorting using the Bray-Curtis similarities. Station names are followed by their classification into assemblages on the basis of the TWINSPAN results.

Station W1 was included in the WM cluster on the basis of the TWINSPAN using the density data and the GAS results. Station V3D was included in the VIG cluster on the basis of the TWINSPAN using the biomass data.

The densities of the various species in the assemblages corresponding to the different clusters are given in detail in Table 2.2 and are summarised in Fig. 2.4. Only fourteen species account for more than 1% of the density in any of the communities thus defined: starfish *Asterias rubens*, brown shrimp *Crangon crangon*, swimming crab *Liocarcinus holsatus*, shore crab *Carcinus maenas*, sand goby *Pomatoschistus minutus*, Lozano's goby *Pomatoschistus lozanoi*, plaice *Pleuronectes platessa*, dab *Limanda limanda*, sprat *Sprattus sprattus*, herring *Clupea harengus*, sandeel *Ammodytes tobianus*, dragonet *Callionymus lyra* and bib *Trisopterus luscus*.

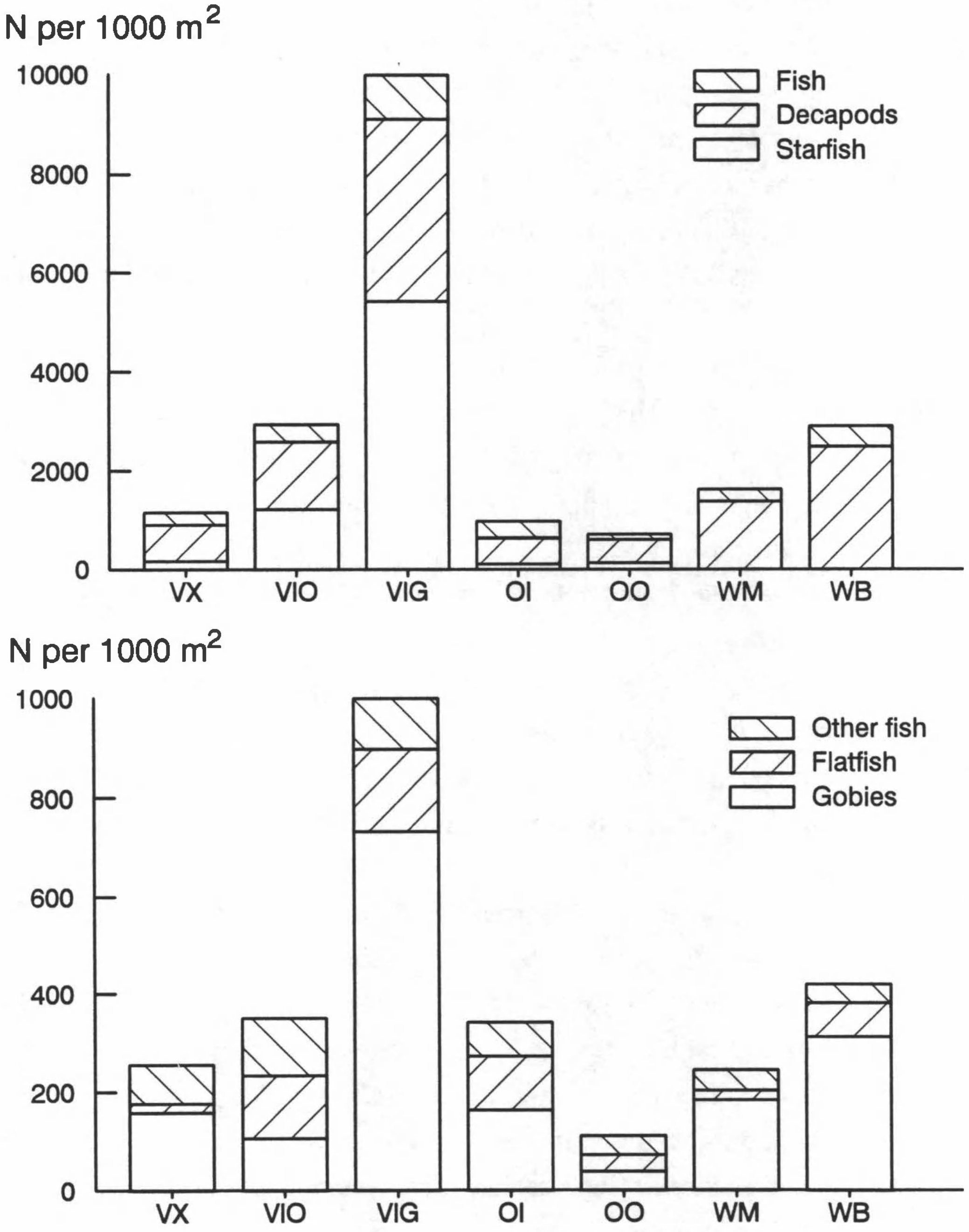


Fig. 2.4. Total density and composition of the different species assemblages for the three main taxonomic groups (top) and the three main fish groups (bottom).

The VX assemblage has the lowest total abundance among the Voordelta clusters (Fig. 2.4). It has few starfish and very few flatfish. It has the highest densities of its indicator species *A. tobianus* and greater sandeel *Hyperoplus lanceolatus* and is the only group of stations in which lesser weever *Trachinus vipera* and scaldfish *Arnoglossus laterna* were recorded (Table 2.2).

The VIO assemblage has an intermediate total abundance. It is poorer than the VIG assemblage for almost all species except for *C. lyra*, *P. platessa*, sole *Solea solea* and its indicator species edible crab *Cancer pagurus*.

The VIG assemblage has the highest total abundance: more than three times higher than in any other assemblage. *C. harengus*, *S. sprattus*, whiting *Merlangius merlangus*, *P. minutus*, *P. lozanoi*, *L. limanda*, *C. crangon*, *L. holsatus* and *A. rubens* plus a host of less abundant species all reach their peak densities in this assemblage.

The OI assemblage has a low total abundance. It has the highest *P. platessa* densities and also the peak densities of a number of species that are rare in the study area as a whole: eelpout *Zoarces viviparus*, sandsmelt *Atherina presbyter*, scad *Trachurus trachurus* and three pipefish species *Syngnathus acus*, *Syngnathus rostellatus* and *Entelurus aequoreus*. It is also the only assemblage in which the black goby *Gobius niger*, the lemon sole *Microstomus kitt* and the lobster *Homarus gammarus* were recorded.

The OO assemblage has the lowest total abundance. Only the poor cod *Trisopterus minutus* has its peak abundance in this assemblage. Both Oosterschelde communities have exceptionally low abundances of *P. lozanoi*. The Oosterschelde is the only area were *T. minutus* and the sea scorpion *Taurulus bubalis*, a rocky shore species, were recorded.

The WM assemblage has an intermediate abundance. Except for the only record of lampern *Lampetra fluviatilis* there are no typical species.

The WB assemblage has a somewhat higher total abundance than the WM assemblage. It has the highest densities of its indicator species flounder *Pleuronectes flesus*. Notable but rare species are twaite shad *Alosa fallax* and mitten crab *Eriocheir sinensis*, both only recorded in this assemblage. The absence of starfish in the Westerschelde is a distinguishing feature. The common goby *Pomatoschistus microps* reaches its highest densities in the Westerschelde.

Biomass composition for the three main groups: fish, decapods and starfish is shown in Fig. 2.5. It can be seen that the dominance of the invertebrate groups in the Voordelta clusters is even stronger than in density terms. Fish are the dominant group only in the Oosterschelde.

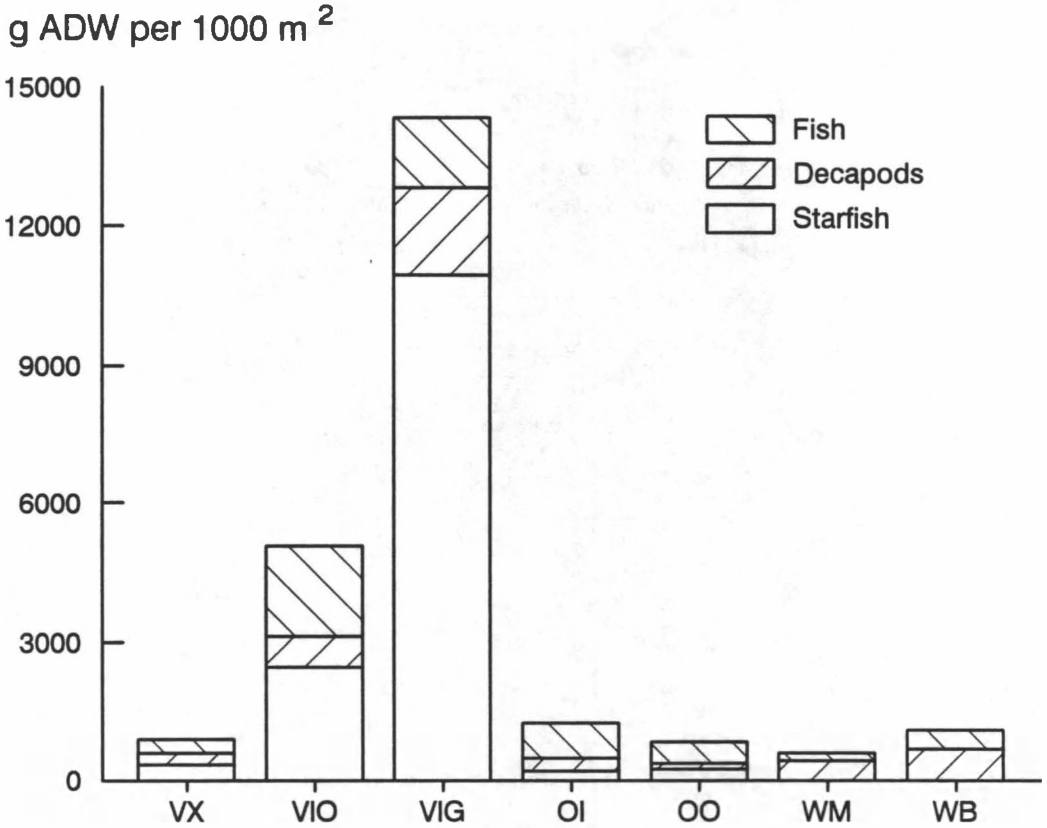


Fig. 2.5. Total biomass and composition of the different species assemblages for the three main taxonomic groups.

Relation to the environmental variables

The total community variability, which corresponds to the distance between the two most extreme stations along the first axis, as measured in units of scale (1 unit scale equals 1 unit standard deviation by definition) in the CA (not depicted) is only 1.2 units. This means a linear response model is most appropriate for the data. Moreover, most species have their optima outside of the range covered by the sampling: the scale of the species scores in the CA is 7.3 times smaller than the scale of the sample scores. Therefore in this study PCA is the method of choice for the ordination with the environmental variables (Jongman *et al.* 1987, Braak & Prentice 1988).

The first PCA axis has an eigenvalue of 0.16, both the second and third axes have eigenvalues of 0.13. In the plain formed by the first and the second PCA axis the sample scores clearly separate the totality of Westerschelde stations from the rest of the Delta area (Fig. 2.6).

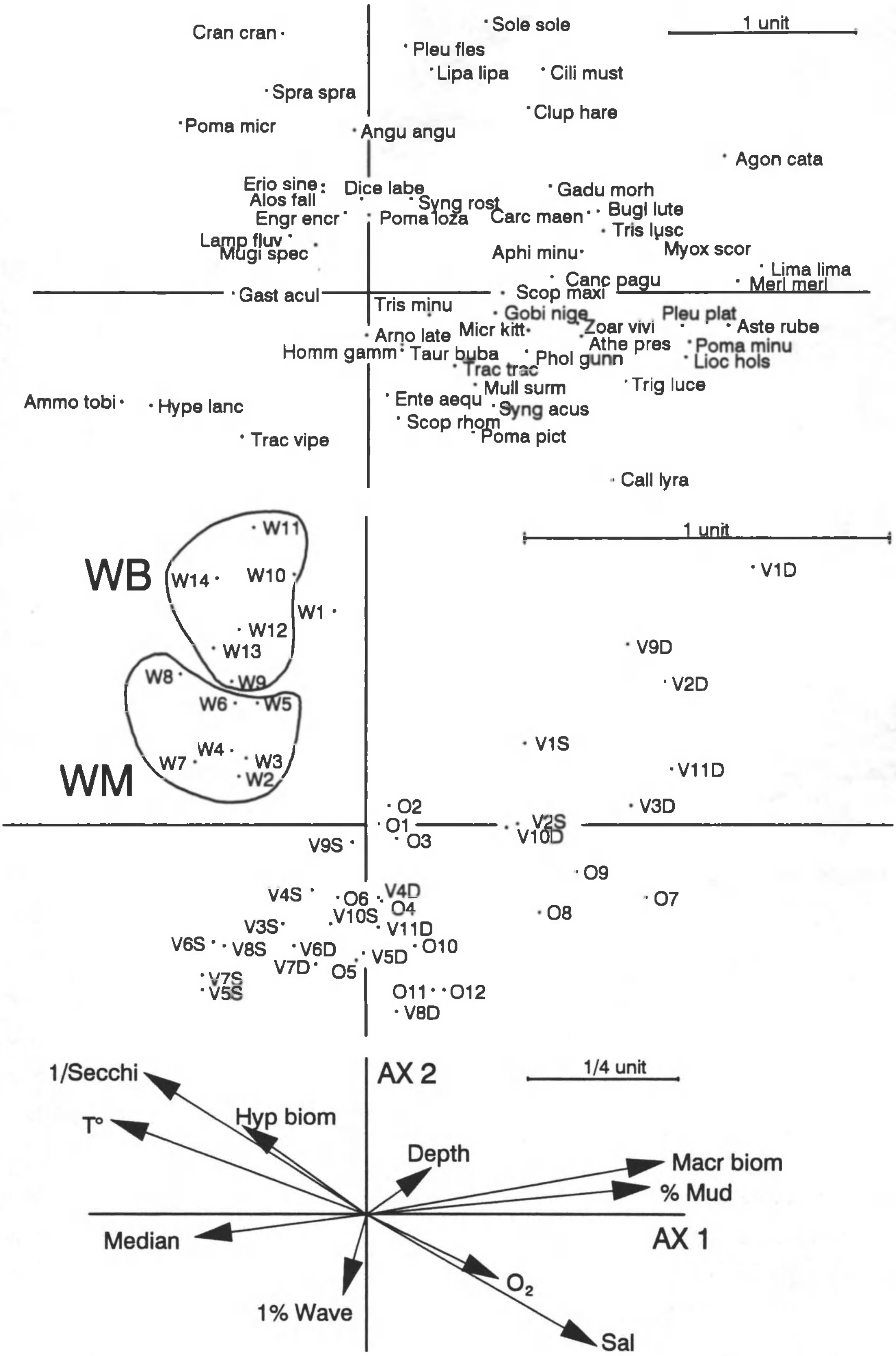


Fig. 2.6. Result of the Principal Component Analysis for the first two axes. The species scores (top), the sample scores (centre) and the environmental biplot (bottom) have different scales.

All Westerschelde stations are located in the left upper quadrant which, in the corresponding species plot, contains *C. crangon*, *S. sprattus*, *P. microps*, eel *Anguilla anguilla*, sea bass *Dicentrarchus labrax*, *A. fallax*, *L. fluviatilis*, Mugilidae species, anchovy *Engraulis encrasicolus*, *E. sinensis* and *G. aculeatus*. Interestingly these species do not necessarily have their highest abundances in these stations but they are a constant and prominent feature of the Westerschelde stations. The stations corresponding to the WB and WM assemblages are separated along the second axis, except for W1 which associates with the WB cluster.

The other stations are plotted as a diagonal string with, at the left lower extreme, the shallow stations at the marine edge of the Voordelta (V3S through V8S), corresponding to the indicator species of the VX assemblage in the lower left quadrant of the species plot. This assemblage, characterised by *A. tobianus*, *H. lanceolatus* and *T. vipera*, has a clear preference for the dynamic sands at the edge of the ebb-tidal delta.

In the central part of the plot there is a mixture of Voordelta and Oosterschelde stations. In the right upper quadrant one finds the stations of the VIG and VIO clusters.

From the environmental biplot it is clear that the first axis correlates strongly with mud content and its covariable macrobenthic biomass. These two variables are negatively correlated to median grain size. The second axis correlates most strongly with the estuarine gradient in the Westerschelde with low water transparency (high 1/Secchi disk depth), high temperature and high hyperbenthic biomass towards the left upper corner and high oxygen content and high salinity towards the lower right.

In the plain formed by the first and third axes of the PCA the stations divide into four major groups (Fig. 2.7): an Oosterschelde cluster which can be separated into the OO and OI clusters, the VI cluster where the VIO (now with station V2S) and VIG clusters can be distinguished, the VX cluster and a tight cluster of Westerschelde stations (except for station W2 which lies close to the VX cluster).

In the species plot the species typical for the Oosterschelde are found in the right upper quadrant. In the right lower quadrant the species closest to the first axis are characteristic for the VIO cluster, the species towards the extreme lower right corner are those typical for the VIG cluster, notably *A. rubens* and *L. holsatus*.

From the environmental biplot it is clear that the third axis shows a strong correlation with the 1% significant wave, which itself is negatively correlated with depth.

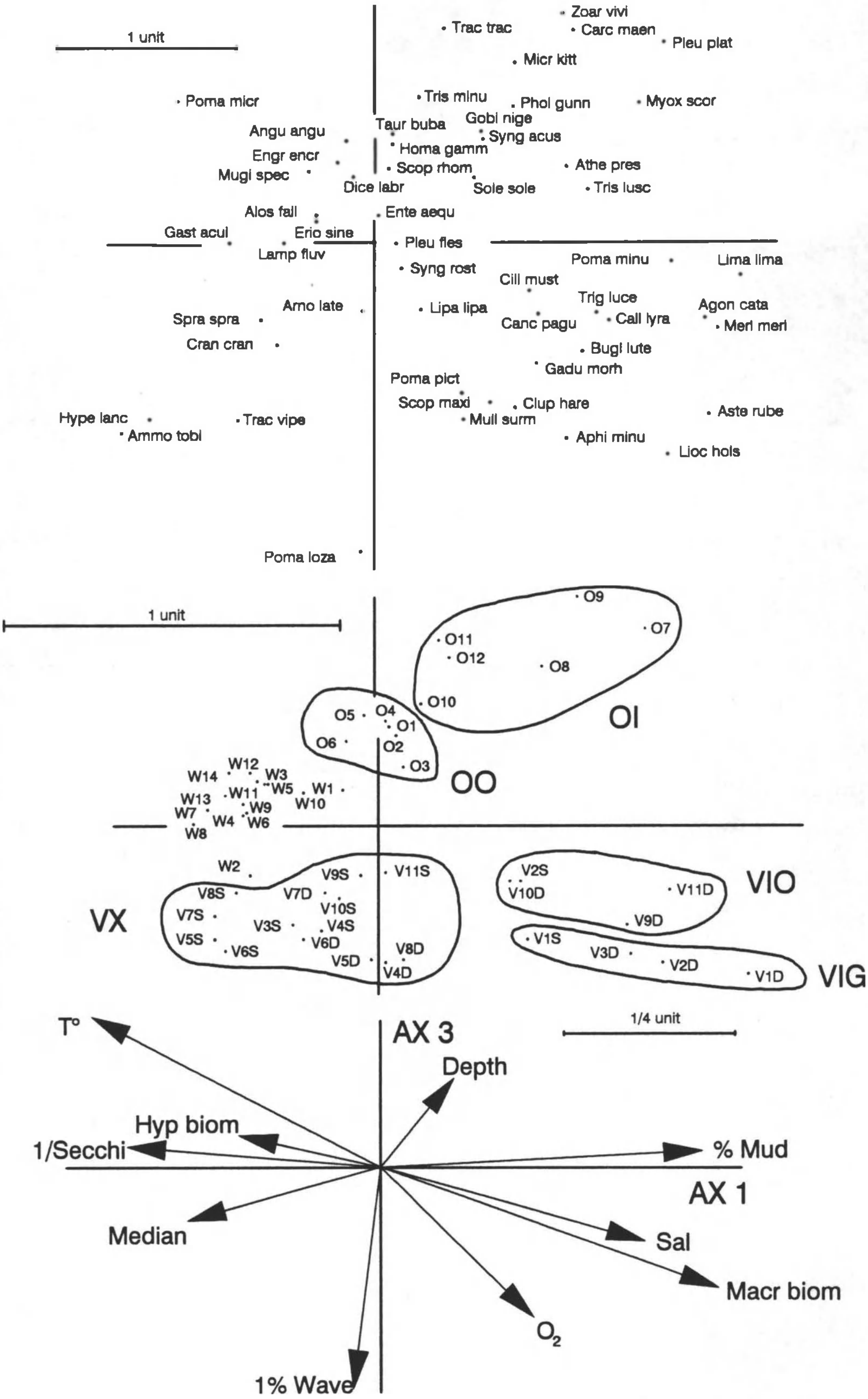


Fig. 2.7. Result of the Principal Component Analysis for the first and third axes. The species scores (top), the sample scores (centre) and the environmental biplot (bottom) have different scales.

Diversity (Fig. 2.8)

The average number of species recorded per station in each assemblage (N_0) is highest in the inshore Voordelta and Oosterschelde assemblages and lowest in the Westerschelde assemblages. Note that, though the highest number of species (41) was recorded in the VX assemblage (Table 2.2) the average number per station (N_0) is lower than in the other Voordelta and Oosterschelde assemblages.

From the diversity measures of higher order the exceptional character of the OI cluster is apparent. In this assemblage a total of 40 species was recorded in only six stations. The high N_1, N_2 and N_∞ measures are mainly due to the locality in the Northern branch of the Oosterschelde (O7,8,9 in Fig. 2.1). The three stations at this locality are dominated by *A. rubens*, *C. crangon* and *P. minutus* and have low densities of a host of other species. The other communities exhibit a steadily decreasing diversity for all higher order measures when moving from seaward to landlocked and finally to estuarine conditions.

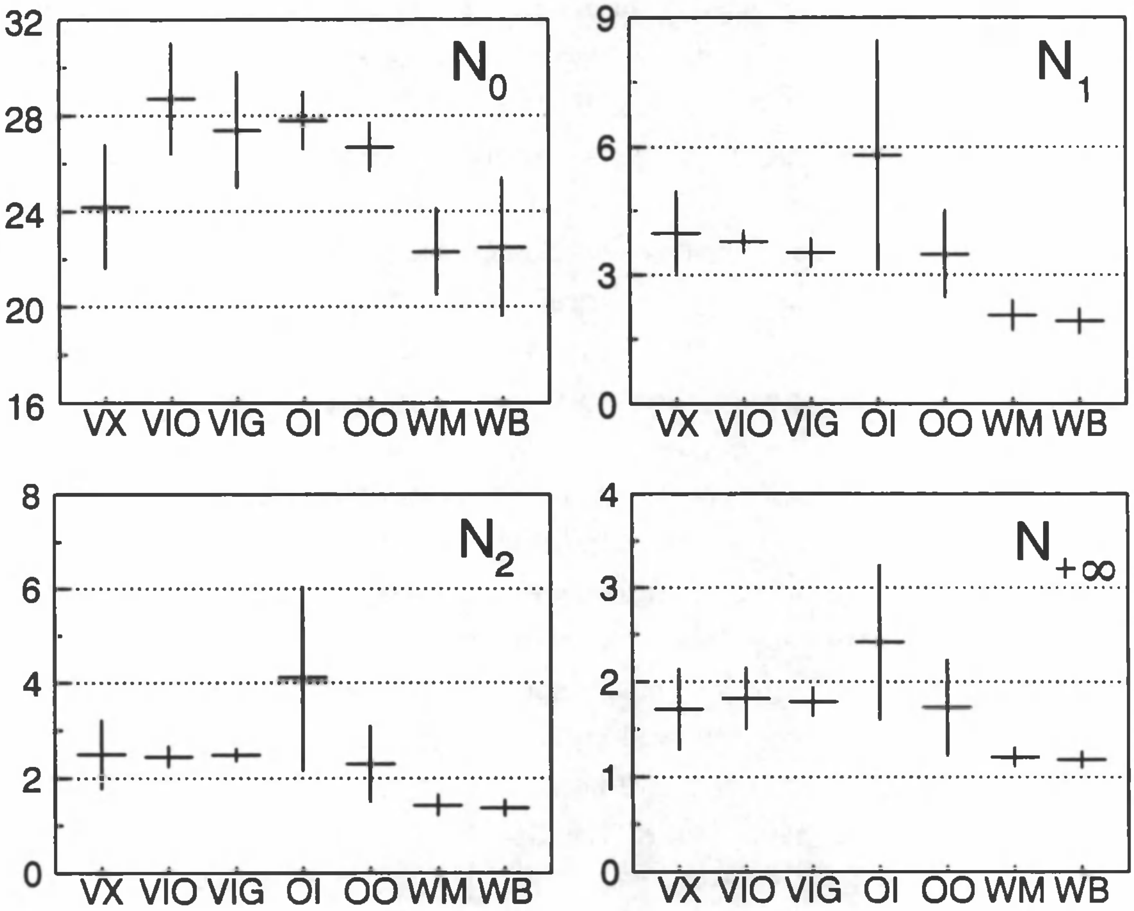


Fig. 2.8. Means of the Hill diversity numbers N_0, N_1, N_2 and $N_{+\infty}$ for the different species assemblages with their standard deviations.

DISCUSSION

The typical beam trawl surveys designed for the monitoring of fishes are also very efficient for catching mobile epibenthic invertebrates. These invertebrates are a dominant component in every assemblage and the information inherent in the occurrence of these animals should therefore be used. The present study also suffers from this partiality, at least for some of the less abundant species. Though every fish was examined in detail, the invertebrates were treated in bulk and only occasionally, e.g. in small catches, were the rarer invertebrates noticed. It seems likely for instance that *Pontophilus trispinosus* and *Portumnus latipes*, though rare, are typical members of the VX community. The exceptionally high diversity of the Oosterschelde, especially as measured by N_1 would also be even more spectacular if all invertebrates found had been quantified. Community structure is, at least partly, determined by species interactions such as competition and predation. These interactions are not limited to either fish-fish or crab-crab but go across taxonomic boundaries. Some of these predatory interactions are structurally important, e.g. shrimp-plaice (Veer 1986), whiting-shrimp (Henderson & Holmes 1989). Evidence on competitive interactions is less conclusive, but many species are known to share the same food (Le Mao 1986, Costa & Elliott 1991). Therefore, it is recommended that future studies reporting primarily on demersal fish include data on the mobile epibenthic invertebrates.

As most fish and epibenthic crustaceans are highly mobile and perform seasonal migrations, obscured by the use of annual means, it is not surprising that the spatial structure found is relatively weak (low eigenvalues). Still, there is a remarkably strong similarity between the species assemblages found in the present study and those defined by Henderson (1989). This is even more amazing if one considers the fact that Henderson's data were collected from the intake screens of powers stations, whilst ours where collected by beam trawl. It is also evident that many of the environmental variables that correlate strongly with the structure of the respective communities are related to 'exposure' in a broad sense. Sediment structure (median grain size and mud content), macrobenthic biomass and wave height either directly or indirectly reflect the hydrodynamics of the overlying water (Pearson & Rosenberg 1987) and have been shown to affect settlement of postlarval fish (Hamerlynck *et al.* 1992, Pihl & Veer 1992) and the efficiency of antipredator behaviour (Tallmark & Evans 1986).

Henderson's 'exposed estuarine' assemblage consists of three species associations that can be found in virtually the same configuration in the plot of the first two principal components (Fig. 2.6). Some species can be found in close association in both studies, e.g. hooknose *Agonus cataphractus*, cod *Gadus morhua* and *T. luscus*. Similarly Henderson's 'sheltered estuarine' assemblage, characterised by *D. labrax*, Mugilidae species and sea snail *Liparis liparis* corresponds to the WS cluster. Two of the species in Henderson's 'sheltered marine' assemblage: *Atherina boyeri* and *G. niger* are typical for the Oosterschelde cluster (considering that the present study classifies all sandsmelts as *A. presbyter*, but see Creech 1991). Within the 'exposed marine' assemblage of Henderson there is some disagreement between the two studies. Whilst *A. tobianus* and *T. vipera* are common to both Henderson's 'exposed marine' assemblage and the VX cluster, his assemblage contains a host of other species typical for the VIO and VIG clusters. According to Henderson (pers. comm.) this is probably due to the fact that no power stations have been built at truly exposed marine sites of the kind occurring in the seaward part of the Voordelta. The highly dynamic, low macrobenthic biomass sands in VX are ideal for burrowing fishes that do not depend on macrobenthos for their food. The planktivorous sandeels need well oxygenated sands in which rapid burrowing to avoid predators is possible (Macer 1966). *T. vipera* is a sit-and-wait predator that burrows to avoid detection by its preferred prey *Pomatoschistus* species (Creutzberg & Witte 1989) which are quite abundant in that area. The close association of *P. lozanoi* to the negative side of the third axis is not due to a clear preference for the exposed sites but is mainly caused by its conspicuous rarity in the Oosterschelde. In contrast to its close relative *P. minutus* it does not seem to be able to establish itself in the Oosterschelde. In summer, when the small juvenile *P. lozanoi* enter the Oosterschelde, water transparencies are at their maximum (often over 4 m Secchi disk depth), they are presumably very effectively eliminated by visual predators such as *T. luscus* (Hamerlynck & Hostens 1993) and *P. minutus* (O. Hamerlynck unpubl. data).

From both studies it appears that inshore marine and estuarine fish communities are strongly structured by their environment. When more data will become available it seems likely that, given a number of important characteristics such as latitude, sediment type, current velocities, wave impact and salinity, quite accurate predictions could be made on the type of fish assemblage expected at a certain site. It is therefore recommended that such environmental variables be recorded when sampling demersal fishes and mobile epifaunal invertebrates. Deviations from the expected assemblage could therefore be indicators of special circumstances either in the positive or in the negative sense.

In the positive sense the richness of the VIG assemblage is probably a result of recent changes in the ebb tidal delta of the former Grevelingen estuary. Since the closure of that estuary in 1971, changes in the current patterns have turned the area into a sink which traps mud, detritus and larvae of fishes, decapods and macrobenthic animals (Hamerlynck *et al.* 1992). It does not necessarily follow that there is a causal relationship between macrobenthic biomass, or any of its covariables, and the occurrence of a certain species assemblage. Still, it is likely that some of the species occurring towards the right end of the species plot, e.g. *L. limanda*, *P. minutus* and *A. rubens*, because of their food preferences, actively seek for localities with a high macrobenthic biomass. The VIO assemblage resembles the VIG assemblage but is less rich. The stations of the VIO assemblage correspond to those parts of the ebb tidal delta of the Oosterschelde where mud has started to accumulate as a consequence of the reduction in current velocities since the completion of the storm surge barrier in 1986.

A typical example of a deviation in the negative sense can be seen in the Westerschelde which is completely devoid of the freshwater species that, in other areas, occasionally venture into waters of higher salinity. Other notable absents are the Salmonidae, and especially the smelt *Osmerus eperlanus*, which is very abundant in estuaries with sufficient oxygen (Wharfe *et al.* 1984). Though a beam trawl is not the most efficient device to catch such fishes, a number of anadromous fish species should be much more common than at present: *L. fluviatilis* was only recorded once, of *A. fallax* three individuals were caught in a single haul and in total less than ten Mugilidae were caught. This is in sharp contrast to their abundance in the Severn (Claridge *et al.* 1986) and two British east coast estuaries (Pomfret *et al* 1991). In 1989, the annual mean oxygen content measured at the Dutch-Belgian border, only a few kilometres upstream from W14, was below 2.5 mg l^{1} (Eck *et al.* 1991). Marine fishes become severely stressed at oxygen levels of less than 4.5 mg l^{-1} (Poxton and Allouse 1982, Marchand in press). It is therefore unlikely that important fish concentrations occur upstream of W14. The low oxygen levels in the freshwater part of the Schelde are presumably the prime cause for the near absence of the freshwater and anadromous species. Two other absents are the starfish *A. rubens* and the eelpout *Z. viviparus*. The first species used to be common in the Westerschelde but has virtually disappeared (Eck *et al.* 1991). The Polychlorobiphenyl- and Cadmium-content of starfish from the Westerschelde are six times higher than the levels in starfish from the Oosterschelde and this seems to affect their reproduction (Besten 1991). The eelpout, a typical estuarine resident which is common in the Tyne and the Forth (Pomfret *et al.* 1991), is very rare in the Westerschelde. Fry survival in this species is known to be negatively affected by mercury (Jacobsson *et al.* 1986, Essink 1989). Though mercury concentrations in the suspended particulate matter of the Westerschelde have decreased to about one third of their former value over the last decade (Eck *et al.* 1991), concentrations in the sediments are still 4 to 25 times higher than North Sea background levels. Similar tests as those performed for starfish could be done with eelpout to prove or disprove this hypothesis.

The second axis in the PCA is clearly influenced by the estuarine gradients in a series of co-variables but none of the variables measured has a particularly strong correlation with this second component of the PCA. There are certainly conflicting cost-benefit aspects for fishes inhabiting the brackish part. For species such as *S. sprattus*, *P. minutus* and *P. lozanoi*, that are abundant in the brackish part and are known to feed predominantly on mysids there (Hamerlynck *et al.* 1990 and O. Hamerlynck unpubl. data), the important mysid concentrations must be attractive. Avoidance of visual predators in the very turbid inner estuary (Blaber & Blaber 1980) is another bonus for those species. The brown shrimp *C. crangon* may profit both from the high turbidity and the large supply of detritus from the river. On the other hand, slow moving fish and invertebrates may be subjected to oxygen stress. For flatfish the situation is certainly less than optimal because of the low macrobenthic biomass.

The third axis is very important in the sense that it neatly separates the assemblages defined, except for the subdivision WM-WB. However, except for the stronger correlation with wave height, there is little difference between the environmental biplots for the second and third axes. Some hidden variable e.g. current velocity may be structurally important.

CONCLUSIONS

As seen from the results of this study multivariate statistical techniques have a great potential as a tool for an increased understanding of the structure of natural communities, even of mobile species. Most studies of fishes and fisheries are either based on areas of convenience, e.g. the nearest estuary or on statistical rectangles, and these do not necessarily correspond to the extent of natural communities. It would make great biological sense to base functional and process studies on entities that can be clearly distinguished on the basis of their species-abundance composition. Datasets that can be used for these exploratory studies exist but they often lie idle in the fisheries research institutes. Most often they are only used for the extraction of data on the stock size or on the imminent recruitment of commercially important species. An exception to this rule is the study by Daan *et al.* (1990) who have been able to define three different types of fish community in the North Sea on the basis of a multivariate analysis of the English groundfish survey data. There are many other datasets, covering vastly greater areas than the present study, e.g. the ICES Demersal Young Fish Surveys (DYFS) or the 'Aurelia' cruises dataset (Creutzberg 1985), whose spatial and temporal structure could be analysed to great benefit.

ACKNOWLEDGEMENTS

Part of this study was financed by Rijkswaterstaat, dienst Getijdewateren and by FKFO grant 2.0086.88. Kris Hostens acknowledges a grant from the IWONL, Paul A. Van Damme acknowledges a grant from the NFWO. Contribution nr. 612 of the Centre for Estuarine and Coastal Ecology, Yerseke.

Chapter 3

The identification of *Pomatoschistus minutus* (Pallas) and *Pomatoschistus lozanoi* (de Buen) (Pisces, Gobiidae)

Hamerlynck, O. 1990. The identification of *Pomatoschistus minutus* (Pallas) and *Pomatoschistus lozanoi* (de Buen) (Pisces, Gobiidae). Journal of Fish Biology 37: 723-728.

ABSTRACT

Sand gobies are extremely abundant in coastal waters and estuaries. *Pomatoschistus lozanoi* tends to be overlooked due to identification problems. This paper summarises the characteristics to distinguish *P. lozanoi* from *P. minutus* and presents a new distinctive feature that allows identification of juveniles from 15-20 mm standard length onward. The known geographic distribution of *P. lozanoi* is extended northward to 53°30'N and southward to 40°N on the coast of Europe. In northern Europe *P. lozanoi* seems better adapted to the estuarine habitat than previously thought.

INTRODUCTION

Sand gobies of the *Pomatoschistus minutus* complex are the most abundant demersal fish in the coastal waters of the continental shore of the North Sea (Redant 1977, Noort *et al.* 1984), the Wadden Sea (Fonds 1973) and the inshore waters of England and Wales (Henderson 1989).

The *P. minutus* complex consists of three species (Webb 1980): *P. minutus* Pallas 1770, *P. lozanoi* de Buen 1923 and *P. norvegicus* Collett 1903. The first two are typically coastal and estuarine and co-occur on shallow sandy bottoms (Hamerlynck *et al.* 1986). In many studies the species are lumped together under *P. minutus* because of identification problems (e.g. Boddeke *et al.* 1986, Doornbos & Twisk 1987, Henderson 1989). This is unfortunate as all three species have a distinct ecology (Fonds 1973, Hamerlynck *et al.* 1986, 1990) and parasite load

(Hamerlynck *et al.* 1989). *Pomatoschistus norvegicus* is a species of offshore mud and coarse shell deposits (Gibson & Ezzi 1981, Miller 1986), and is thus unlikely to occur with the other two.

The pattern of the sensory papillae of the modified lateral line system on the head provides the best key to identification (Miller 1986). In many instances, especially in juvenile fish, damage to the papillae during capture renders the pattern invisible. Checking the pattern is also time consuming. This paper summarises the known characteristics and presents a new distinctive feature in the pigmentation pattern that allows correct identification of most specimens of both species from 15-20 mm standard length (SL) onward.

MATERIAL AND METHODS

From 1984 to 1989 more than a 100 000 *Pomatoschistus* were examined from the Belgian, Dutch, German and Danish coastal waters of the North Sea, the Wadden Sea, the Westerschelde and Oosterschelde estuary, the saline lake Grevelingen, Scottish waters and the Portuguese coast. The juvenile gobies of both species, used for the drawings in this paper were obtained on 11 August 1986 with a fine mesh 2 m beam trawl in the mouth of the Westerschelde. The fish were anaesthetised in a Benzocaine (ethylamino-4-benzoate) solution in sea water and preserved in neutralised formaldehyde 7% final concentration. For analysis of the papillary pattern on the head the fish are placed under water in a petri dish and examined under a dissecting microscope. Strong lighting from the side, along the length axis of the fish, is used in order to create shadows behind the papillae. This increases the visibility of the papillae. All lengths are standard lengths.

RESULTS AND DISCUSSION

The study of length-frequency distributions and gonadosomatic indices confirms the finding of Fonds (1973) that the species have different spawning periods. In the Belgian coastal area this is from March to June for *P. minutus*, from June to August for *P. lozanoi*. This means that small juvenile gobies caught in the Belgian and Dutch coastal waters in May and June are *P. minutus*, those in September and October are *P. lozanoi*. In July and August juveniles of less than 35 mm length of both species co-occur. In Portuguese waters spawning periods seem to be three months earlier in both species (F. Moreira pers. comm., O. Hamerlynck unpubl. data).

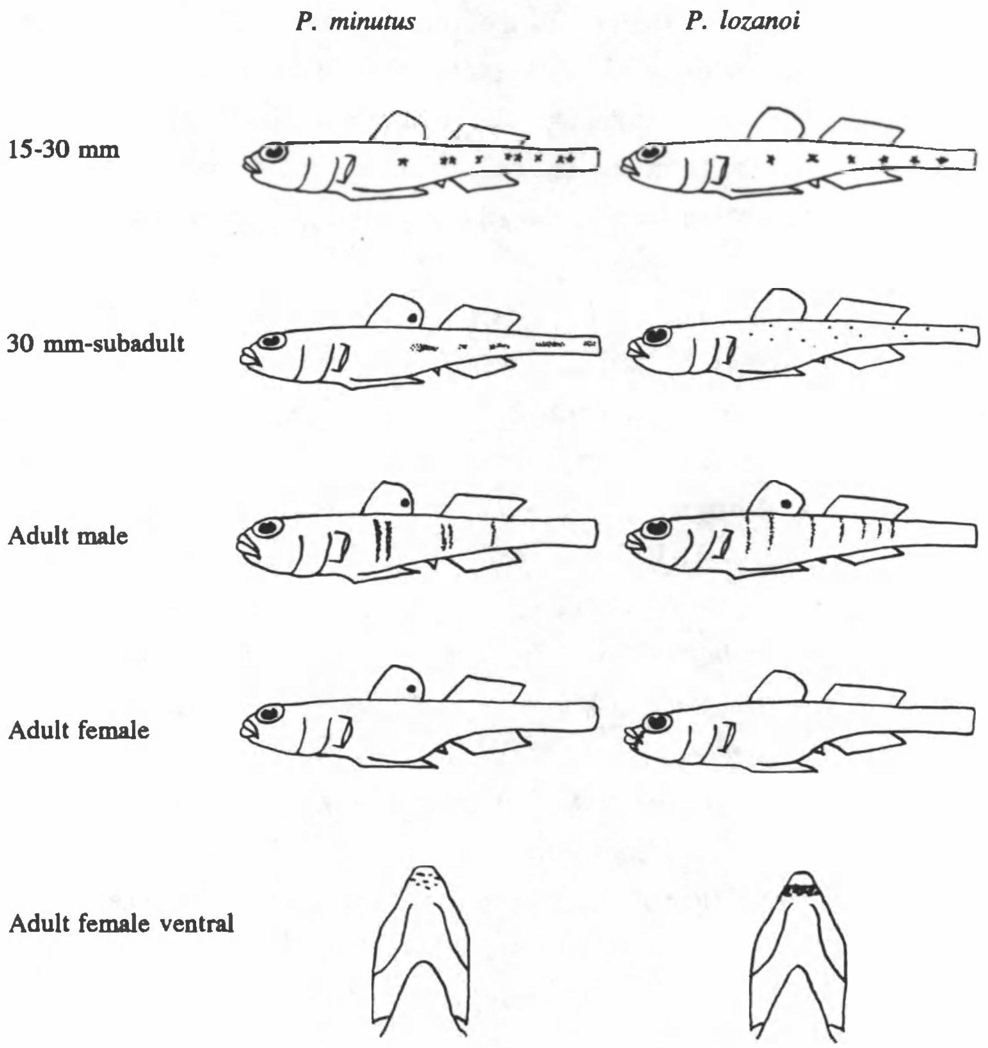


Fig. 3.1. Schematic representation of the main characteristics used for the identification of *Pomatoschistus minutus* and *P. lozanoi* at different sizes and when spawning. Pectoral and tail fins are not shown. The size of the chromatophores in the 15-30 mm size class is greatly exaggerated.

POMATOSCHISTUS MINUTUS

This species occurs on inshore sand and muddy sand in the eastern Atlantic, typically to about 20 m depth (Miller 1986). Maximal size in our samples is 75 mm SL. Juveniles occur quite high up in estuaries even at salinities as low as 5‰ (O. Hamerlynck unpubl. data). It is versatile microcarnivore feeding on a variety of benthic and epibenthic animals (Hamerlynck *et al.* 1986). Spawning is from March to June in the North Sea (Fonds 1973), from January to April in Portuguese waters (F. Moreira pers. comm.).

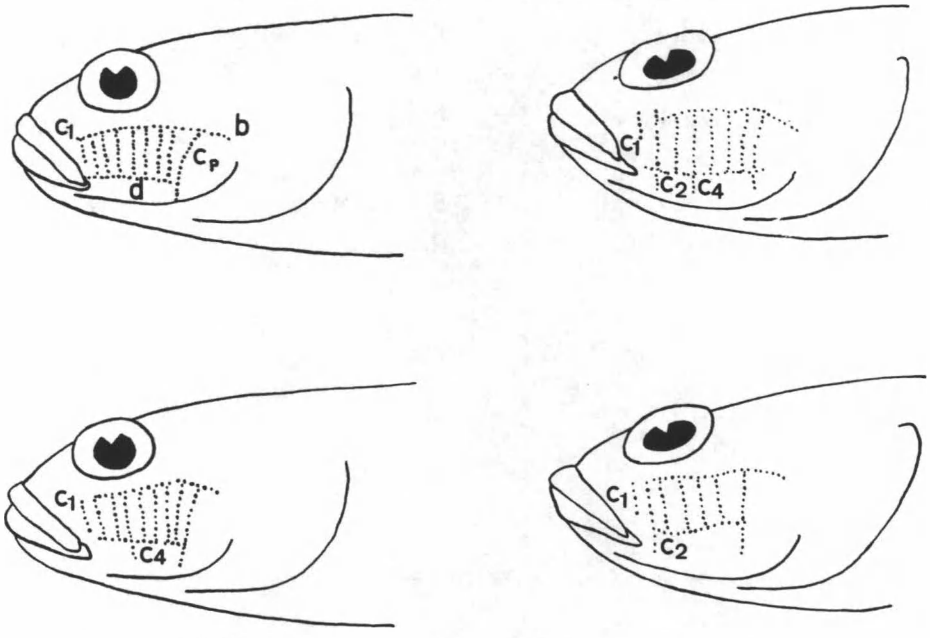
In juveniles of 15-30 mm SL the dorsal half of the fish usually shows extensive pigmentation with small black spots. The lateral line has a row of large single and double radiating chromatophores (Fig. 3.1). Typically there are double chromatophores under the front and tail ends of the second dorsal fin. Most often the spot midway between the tail end of the second dorsal and the base of the tail fin is also double.

When fish reach a size of 30-35 mm SL the black spot on the first dorsal fin becomes prominent and is the easiest criterion for identification until the appearance of spawning pigmentation. The general aspect is quite dark due to a reticulate pigmentation of the dorsal half and a series of diffuse spots along the lateral line. When in doubt, e.g. damaged first dorsal fin and little pigmentation, the pattern of the papillae on the head should be checked. There are many patterns intermediate between the typical patterns as described by Webb (1980) and used in the identification key by Miller (1986). The best criterion is the second c-row: if this continues below the horizontal d-line it is a *P. lozanoi*, if it does not it is a *P. minutus* (Fig. 3.2).

Ripe *P. minutus* males show two double dark vertical bars on the flank, besides some fainter dark lines. Ripe *P. minutus* females have much less pigmentation on the chin than *P. lozanoi*, there is no clear line between the eye and the mouth.

POMATOSCHISTUS LOZANOI

This species occurs inshore (to 70-80 m) and off the mouth of estuaries (Miller 1986). Maximal size in our samples is 65 mm SL. It feeds mainly on mysids, pelagic copepods and juvenile *P. minutus* (Hamerlynck *et al.* 1990). In most places where *P. minutus* occurs and the species has been looked for by experienced observers *P. lozanoi* is also present. In addition to the sites shown in Miller (1986) the species has been found on the west coast of Portugal at Figueira da Foz (40°N), on both the west and east coast of Scotland, and in German and Danish coastal waters at least to 50°30'N in the North Sea. In fact *P. lozanoi* has been found in all the localities sampled. Thus it is likely to have been overlooked elsewhere. In the Westerschelde the species is as common as *P. minutus* and occurs in the same salinity range (O. Hamerlynck unpubl. data). The species also occurs quite high up the Severn Estuary (Claridge *et al.* 1985). This indicates a more estuarine character than suggested by Fonds (1973), who considered the species to be neritic, avoiding estuaries. In southern Europe however *P. lozanoi* may avoid estuaries as the species was not found in an intensive study of the Tagus Estuary (F. Moreira pers. comm.)


Typical *P. minutus*

Typical *P. lozanoi*

Atypical *P. minutus*

Atypical *P. lozanoi*

Fig. 3.2. Typical and atypical papillary patterns of *Pomatoschistus minutus* and *P. lozanoi*. For terminology of the head lateral-line system see Miller (1986).

The general appearance is more slender and much less pigmented than *P. minutus*. Living animals of all sizes are rather translucent and show diffuse reddish spotting. Formalin or alcohol preserved individuals usually have hardly any pigmentation on their dorsal half, except when spawning.

In juveniles of 15-30 mm SL the spots on the lateral line are characteristically single chromatophores, often mere dots or altogether absent (Fig. 3.1).

Unripe fish over 30 mm do not show the reticulate pigmentation of *P. minutus* and lack the black spot on the first dorsal fin. The continuation of the second c-row of papillae under the horizontal d-row, just behind the corner of the mouth is diagnostic (Fig. 3.2).

Table 3.1. Summary of the most important differences between *P. minutus* and *P. lozanoi*.

	Character	*P. minutus*	*P. lozanoi*
General	Papillae	Second c-row not below d	Second c-row below d
15-30 mm	Lateral line	Double spots	Single spots
	Dorsal half	Pigmented	Unpigmented
30 mm-subadult	First dorsal	Black spot	No black spot
	Dorsal half	Reticulated	Little or no pigmentation
Spawning male	Flank	Few double bands	Seven to nine single bands
Spawning female	Face	No 'moustache'	'Moustache'
	Chin	Slight pigmentation	Dark blotch

Ripe males show seven to nine, more or less regularly spaced dark vertical bars. These are not grouped in pairs as in *P. minutus*, although the first two are closer to one another than the more caudal ones. Ripe females have a characteristic 'moustache': a dark line extending from the eye to the mouth. This dark pigmentation is continued under the chin as a very dark aggregation of pigment (Fig. 3.1).

Though ripe females lack a truly black spot on the first dorsal, the pigmented bands on this fin may be confusing.

SUMMARY

P. minutus and *P. lozanoi* co-occur abundantly on most shallow marine soft bottoms of the west coast of continental Europe at least from 40°N in Portugal to 55°30' N on the Danish west coast. They also co-occur in the estuaries of northern Europe and around the British Isles.

The main identification criteria are summarised in Table 3.1. Small juveniles of both species, below 15-20 mm, as a rule show hardly any pigmentation. When they do they are almost certainly *P. minutus*. Unpigmented individuals at these sizes cannot be identified at present. Conceivably this is possible by the use of quadratic discriminant functions (Froese 1988). From 15-20 mm to 30-35 mm SL nearly all individuals can be positively assigned to either *P. minutus* (double spots) or *P. lozanoi* (single spots). Above 30-35 mm the black spot on the dorsal fin of *P. minutus* becomes diagnostic. Ripe females of *P. lozanoi* have much darker pigmentation around the mouth than *P. minutus,* especially under the chin. In ripe males the pigmentation pattern reflects the difference in chromatophores used in the identification of the juveniles: *P. minutus* males show dark double bands on the flanks. In *P. lozanoi* these bands are single and more numerous.

ACKNOWLEDGEMENTS

Contribution no. 509 of the Delta Institute of Hydrobiological Research, Yerseke.

Chapter 4

The parasites of two sympatric gobies *Pomatoschistus minutus* and *P. lozanoi* in the Belgian coastal waters

Hamerlynck, O., Geets, A. & Damme, P.A. van 1989. The parasites of two sympatric gobies, *Pomatoschistus minutus* and *P. lozanoi* in the Belgian coastal waters. In: Wouters, K. & Baert, L. (Eds.). Proceedings of the Symposium 'Invertebrates of Belgium'. KBIN, Brussels: 27-30.

ABSTRACT

Sand gobies were obtained from the bycatch of a commercial shrimp trawler in the Westdiep area, Southern Bight of the North Sea. Prevalence and infection rate of their helminth and crustacean parasites were recorded. Both species, *Pomatoschistus minutus* and *P. lozanoi*, are final hosts for *Lernaeocera minuta* and *Asymphylodora demeli*. The higher infection rate of *A. demeli* in *P. minutus* juveniles may be linked to the difference in food resource use between the goby species. Both species are also intermediate hosts to *Bothriocephalus scorpii* and *Hysterothylacium aduncum*, important parasites of commercial fish species.

INTRODUCTION

Sand gobies of the *Pomatoschistus minutus* complex (Webb 1980) are the most abundant fish in the Belgian coastal waters (Redant 1977). Two species from this complex, *Pomatoschistus minutus* Pallas 1770 and *P. lozanoi* de Buen 1932, occur sympatrically in the Westdiep area west of Nieuwpoort, and show a distinctly different food resource use: *Pomatoschistus minutus* feeds mostly on benthic and epibenthic animals, while *P. lozanoi* specialises on mysids (Hamerlynck *et al.* 1986). In the North Sea west of Texel, *Pomatoschistus minutus* spawns from March to June, *P. lozanoi* from May to August. They are repeat spawners, producing several batches of eggs. Nearly all adults of both species die within a few weeks after spawning (Fonds 1973). In the Westdiep area young *P. minutus* appear in the catches in July, young *P. lozanoi* in August (Hamerlynck *et al.* 1986).

Most studies of parasites of fish populations have been limited to commercially important fish stocks. The present knowledge covers less than 2% of fish species (Kinne 1984). The parasite fauna of *Pomatoschistus minutus* has been described in the Baltic by Markowski (1935a) and Koter (1962). They noted the occurrence of 4 species of digenean trematodes, 4 species of cestodes, 2 species of acanthocephalans and two species of nematodes. Fonds (1973) recorded *Asymphylodora demeli* Markowski 1935, *Bothriocephalus scorpii* Müller 1776 and *Hysterothylacium aduncum* (= *Contracaecum aduncum*) Rudolphi 1802 from the stomachs of *P. minutus* and *P. lozanoi* from the Wadden Sea.

This paper provides data on the incidence and infection rate of helminth and crustacean parasites in sand gobies from the Westdiep area.

MATERIALS AND METHODS

Monthly samples were obtained from the bycatch of a commercial shrimp trawler operating in the Westdiep-Trapegeer area off Nieuwpoort from May through December 1984, and in June and August 1985. In April 1985 fish from the same area were obtained from the Fisheries Research Institute, Ostend.

On board all fish were anaesthetised in a Benzocaine solution in sea water and preserved in neutralised formaldehyde (7% final concentration) within 15 minutes after capture. Some 1400 fish, out of a total of 12725, were examined for parasites on the gills, in the abdominal cavity and in the gut. The number of parasites per individual was recorded.

RESULTS

Four different species of parasites, the life cycle of which is given in Table 4.1, were found in *Pomatoschistus minutus* and *P. lozanoi*. Adult and mature specimens of *Asymphylodora demeli* were found in the intestine and the rectum. Larval stages (plerocercoids) of the cestode *Bothriocephalus scorpii* were collected from the stomach and immature specimens of the nematode *Hysterothylacium aduncum* were recovered from the abdominal cavity. Adult *Lernaeocera minuta* Scott 1900 (Crustacea, Copepoda) were attached to the gills and the gill arches, only rarely to the pectoral fins.

Table 4.1. Life cycle of the helminth and crustacean parasites of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* (after Markowski 1935a, 1935b, Reimer 1973, Kinne 1984).

Parasite	1 st interm. host	2 nd interm. host	Final host
Asymphylodora demeli (Trematoda)	unknown	Several spp. of gastropods	*P. minutus* *P. lozanoi* *Rutilus rutilus* *Nereis diversicolor* (Annelida, Polychaeta)
Bothriocephalus scorpii (Cestoda)	*Eurytemora hirundo* (Crustacea, Copepoda)	*P. minutus* *P. lozanoi*	*Pleuronectes flesus* *Rhombus maximus* *Myoxocephalus scorpius*
Hysterothylacium aduncum (Nematoda)	several spp. of invertebrates	*P. minutus* *P. lozanoi* (and other spp. of fishes)	Several spp. of fishes
Lernaeocera minuta (Custacea, Copepoda)	unknown		*P. minutus* *P. lozanoi*

The prevalence and mean intensity of infection of *Pomatoschistus minutus* and *P. lozanoi* with *A. demeli* is shown in Table 4.2. It can be seen that the younger *P. minutus* (caught in July and August 1984) harboured a high number of *Asymphylodora* specimens. Spawning fish of this species show a high prevalence but a relatively low intensity of infection with *A. demeli*. Older *P. lozanoi* are more heavily infected with *A. demeli* than younger fish. The highest infection level was reached in August 1985 (27 parasites per fish).

In Table 4.3 the infection level of *P. minutus* and *P. lozanoi* with *B. scorpii*, *H. aduncum* and *L. minuta* is shown. In autumn a relatively low number of *P. minutus* is infected with a high number of *B. scorpii*. *H. aduncum* is present in the abdominal cavity throughout the year, but highest infection levels were recorded in ripe *P. minutus* in spring. *L. minuta* seems to infect older, post-spawning *P. minutus*.

Table 4.2. Prevalence and mean intensity of infection of *Asymphylodora demeli* in the gobies *Pomatoschistus minutus* and *Pomatoschistus lozanoi*.

	Pomatoschistus minutus				*Pomatoschistus lozanoi*			
Date	Number of fish	Mean length (mm)	Prevalence (%)	Mean intensity (N/fish)	Number of fish	Mean length (mm)	Prevalence (%)	Mean intensity (N/fish)
17.05.84	51	53.8	98.0	14.1	53	48.7	96.3	8.7
20.07.84	82	34.8	96.0	136.7	79	48.0	64.6	1.8
17.08.84	30	46.6	92.9	101.6	30	47.1	86.7	5.8
28.09.84	338	48.2	77.2	29.3	111	40.7	47.8	0.7
30.10.84	90	42.4	44.5	11.9	80	41.3	27.5	0.4
13.12.84	60	44.7	41.6	6.9	36	45.4	41.7	0.4
18.04.85	22	47	90.9	4.0	30	46.9	93.2	3.4
09.08.85	56	43.8	94.6	65.4	59	44.5	98.4	27.2

Because of the smaller number of parasite specimens collected from *P. lozanoi* no distinct seasonal pattern in the occurrence of parasites can be found. However, it is clear from Table 4.3 that *B. scorpii* is particularly abundant in the younger stages, while infection levels for *H. aduncum* and *L. minuta* are low during that period. The infection level with *L. minuta* reaches a maximum in late spring (June 1984).

DISCUSSION

Infective stages of parasites enter the appropriate host most often through the food web (Kennedy 1975). This implies that infection levels may be closely related to the availability in the plankton or the benthos of specific food items which serve as intermediate hosts. Seasonal patterns in incidence of infestation and in parasite burden may then be the result of the seasonal occurrence of intermediate hosts.

Asymphylodora demeli infects juvenile *P. minutus* massively in early summer (July 1984). The early postlarvae of both goby species are zooplanktivores (Hamerlynck unpubl. data). As juvenile *P. lozanoi* are much less affected, this would suggest the intermediate host almost disappears from the zooplankton before *P. lozanoi* juveniles start to hatch, thus before June. The first intermediate host in *Asymphylodora* species remains unknown. Metacercariae were found in a number of gastropods belonging to the brackish water fauna (Markowski 1935a). The different infection rate of *P. minutus* and *P. lozanoi* with *A. demeli* could be due to the difference in food resource use and not to the temporal segregation of spawning. The parasite is found in the Baltic, in the Southern Bight of the North Sea and in gobies from the west coast of Portugal (Hamerlynck unpubl. data), thus *A. demeli* seems to be very widespread indeed. Elucidation of its life cycle could provide an explanation for the zoogeography of the parasite species.

Table 4.3. Prevalence of *Bothriocephalus scorpii*, *Hysterothylacium aduncum* and *Lernaeocera minuta* in *Pomatoschistus minutus* and *Pomatoschistus lozanoi* (in %). the mean intensity of infection (number of parasites/infected fish) is given between brackets.

	Pomatoschistus minutus				*Pomatoschistus lozanoi*			
Date	Number of fish	*B. scorpii*	*H. aduncum*	*L. minuta*	Number of fish	*B. scorpii*	*H. aduncum*	*L. minuta*
17.05.84	51	7.8 (1.0)	21.6 (1.7)	39.2 (1.7)	53	5.7 (1.3)	15.1 (1.0)	9.4 (1.2)
20.07.84	82	0	4.8 (1.0)	0	79	0	16.5 (1.6)	10.1 (1.3)
17.08.84	30	3.3 (1.0)	3.5 (1.0)	0	30	0	13.3 (1.7)	3.3 (1.0)
28.09.84	338	14.3 (1.8)	2.0 (1.0)	0.8 (1.0)	111	19.8 (1.3)	1.8 (1.0)	0.9 (1.0)
30.10.84	90	13.3 (1.3)	6.7 (1.0)	1.1 (1.0)	80	18.8 (1.2)	2.5 (1.0)	0
13.12.84	60	10.0 (1.0)	10.0 (1.2)	5.0 (1.0)	36	25.0 (1.2)	2.8 (1.2)	0
18.04.85	22	9.1 (1.0)	13.6 (1.0)	4.5 (1.0)	30	20.0 (1.2)	6.7 (1.0)	0
01.06.85	-	-	-	-	21	21.7 (1.9)	1.7 (1.0)	25.0 (1.2)
09.08.85	56	0	3.6 (1.0)	0	59	11.9 (1.3)	10.2 (1.2)	8.5 (1.0)

Infection rates of *P. minutus* and *P. lozanoi* with *Bothriocephalus scorpii* are highest in autumn. The intermediate host, *Eurytemora hirundo*, mentioned by Markowski (1935b) is never recorded in any stomach, *Eurytemora* species being restricted to brackish habitats. Probably a marine calanoid copepod could also serve as intermediate host.

The complete life cycle of *Lernaeocera minuta* remains unknown. According to Mann (1964) *L. minuta* causes a loss of weight, induces obvious changes in fat and water content of muscle and other tissues and lowers the haemoglobin content when attached to *P. minutus*. From our results it may be suggested that *L. minuta* typically invades spent *P. minutus*, exacerbating the low condition due to spawning activities.

CONCLUSIONS

Sand gobies are the final hosts for *Lernaeocera minuta* and *Asymphylodora demeli*, from the Baltic down to Portugal. The life cycles of both these parasites have not yet been elucidated. The two other parasite species found, *Hysterothylacium aduncum* and *Bothriocephalus scorpii*, both have piscivorous fish as final hosts and as gobies constitute one of the most important food sources for a number of commercial fishes (Redant 1977) they may be the main intermediate host in the Belgian coastal area.

ACKNOWLEDGEMENTS

This research was supported by the NFWO (FKFO-PROJECT no. 2.0086.88). L. Bogaert and Dr. F. Redant are acknowledged for their assistance.

Chapter 5

The trophic position of *Pomatoschistus lozanoi* (Pisces, Gobiidae) in the Southern Bight

Hamerlynck, O., Vyver, P. van de & Janssen, C.R. 1990. The trophic position of *Pomatoschistus lozanoi* (Pisces, Gobiidae) in the Southern Bight. In: Barnes, M. & Gibson, R.N. (Eds.). Trophic relationships in the marine environment. Proceedings of the 24th European Marine Biology Symposium. Aberdeen University Press, Aberdeen: 183-190.

ABSTRACT

Sand gobies of the genus *Pomatoschistus* are the most abundant fish in the shallow coastal areas of the North Sea. *Pomatoschistus lozanoi* has a somewhat specialized diet feeding mainly on a few pelagic and hyperbenthic species: *Temora longicornis*, *Schistomysis* species and juvenile *Pomatoschistus minutus* together supply more than 70% of the energy in most months. In August the species shifts to benthic and epibenthic feeding: juvenile *Crangon crangon* and radioli of *Lanice conchilega* are the main food. Numerically the same species are dominant in most months. In December and August the amphipods *Microprotopus maculatus* and *Pariambus typicus*, in June cypris larvae and the harpacticoid *Microarthridion littorale* are important numerically. Thus *Pomatoschistus lozanoi* is a remarkable demersal fish, dependent throughout its life on the secundary and tertiary production in the water column.

INTRODUCTION

The gobiid fish *Pomatoschistus lozanoi* de Buen 1923, classified with *Pomatoschistus norvegicus* in the *Pomatoschistus minutus* complex (Webb 1980), is common on sandy bottoms in most North-eastern Atlantic coastal areas at least South to Portugal, North to the Wadden Sea and around the British Isles (Miller 1986). Many recent studies still ignore the existence of *Pomatoschistus lozanoi* despite the fact that the species is present in the area studied, e.g. Doornbos & Twisk (1987), Boddeke *et al.* (1986), Henderson (1989), or only split up the species complex for part of the study period, e.g. Claridge *et al.* (1985). Without detailed knowledge of the ecology of both species, lumping them in a "sand gobies" superspecies seems unwise. Fonds (1973) suggested that in comparison with the sympatric *Pomatoschistus minutus*, *P. lozanoi* is a more neritic species, that avoids estuaries because of a lower tolerance for low temperature and salinity, that feeds on nekto-benthos rather than benthos and that has a different spawning season: May to August, rather than March to June. This study was undertaken to establish the trophic position of *Pomatoschistus lozanoi* in the food web of a shallow coastal area.

MATERIALS AND METHODS

Gobies were obtained more or less monthly from the bycatch of a commercial shrimp trawler "O62" operating at 10-20 m depth in the Westdiep-Trapegeer area (Fig. 5.1), from May through December 1984. In April 1985 fish were obtained from the same area through the Fisheries Research Institute Ostend. In June and August 1985 two more samples were obtained from the O62. Mesh size is 20 mm stretched in the cod end. On board all fish are immediately anaesthetized in a Benzocaine (Ethylamino-4-benzoate) solution in sea water to prevent regurgitation of stomach contents. Within 15 minutes after capture the fish are preserved in neutralized formaldehyde 7% final concentration. At least three months after capture standard length is measured and fish are divided into 5 mm length classes. From the most abundant size classes a maximum of 30 fish is selected at random for stomach analysis. All food items in the entire gasto-intestinal tract, excluding the rectum, are identified, if possible, to species level. For calanoids, harpacticoids and chaetognaths assigned Ash Free Dry Weight (AFDW) values are used. All other animals are measured, and their AFDW prior to digestion is calculated from regressions established for animals from the same area (Appendix). The original size of incomplete prey is calculated from regressions relating unbroken parts, e.g. a telson or an antennal scale to total length. For the radiole crowns of *Lanice conchilega* a visual volumetric estimate is compared with a volume of undigested radioles of known AFDW. Only species representing more than 4% either numerically or gravimetrically in a single size class or a single month are discussed (Field *et al.* 1982).

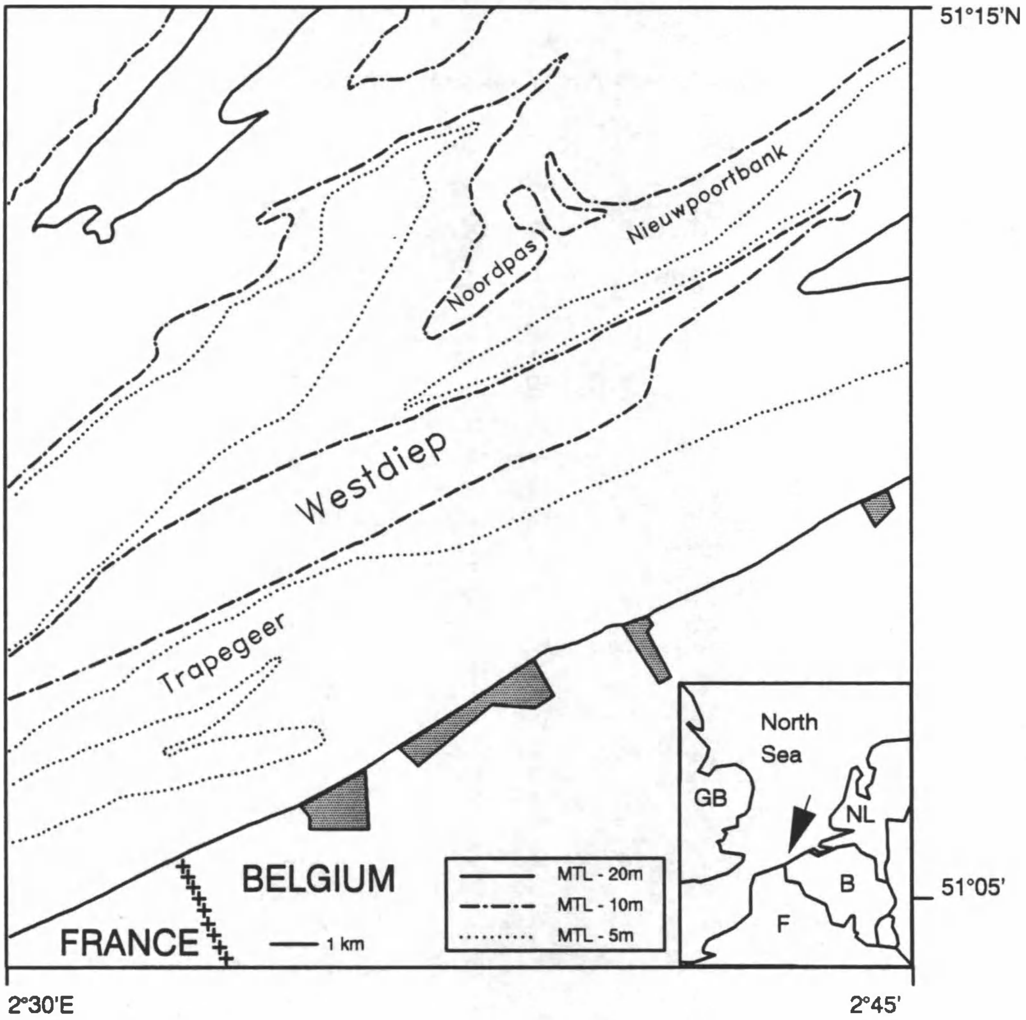


Fig. 5.1. Map of the study area in the Southern Bight of the North Sea (MTL is Mean Tidal Level).

RESULTS

A total of 3327 fish were examined and 537 stomachs were analysed. It is impossible to estimate density and biomass from this kind of data, they will be the subject of other papers. There is very little variation in mean length of the gobies throughout the year as the lower limit of gear selection is close to the maximum size of the fish. Data on the parasites found in the fish have been published elsewhere (Hamerlynck *et al.* 1989).

Results are presented in a hypothetical sequence from first capture of the juveniles in September to the last 1+ adults caught in August, although the samples were taken in a different order and contain fish from different year classes (1983 and 1984). The August result is a mixture of samples from 1984 and 1985.

Gravimetric food composition is shown in Table 5.1 and summarized in Fig. 5.2. In autumn the O-group *Pomatoschistus lozanoi* derive nearly all their energy from mysids, of which more than 90 % are *Schistomysis spiritus*. In the following spring the maturing fish feed mainly on juvenile *Pomatoschistus minutus*, *Temora longicornis*, gammaridean amphipods and some mysids. Larvae of Clupeidae, mainly *Clupea harengus* are important in June.

Table 5.1. Size classes of fish and number of stomachs examined, number of prey items and numerical and gravimetric food composition (main species) over the year.

Month	Sep	Oct	Dec	Apr	May	Jun	Jul	Aug
Fish size (mm)	25-55	35-50	40-50	45-50	45-55	40-50	40-55	40-50
Number of stomachs	110	81	36	30	52	60	79	89
Number of items	4426	1236	135	955	1491	2805	286	449
Prey species	Numerical percentage							
Temora longicornis	85	68	35	98	93	17	3	7
Centropages species						1	19	1
Microarthridion littorale						58		
Cirripedia larvae				1		21		
Microprotopus maculatus	5	1	19				2	14
Pariambus typicus	3	1	14				5	25
Pseudocuma longicornis		1	7					18
Schistomysis spiritus	5	27	11		1		60	
Crangon crangon							1	10
Lanice conchilega			5				3	20
Prey species	Gravimetric percentage							
Temora longicornis	16	3	2	22	20	1		
Gammarus species					18			
Diastylis species						4		
Schistomysis spiritus	74	96	74		18		69	
Gastrosaccus spinifer					7			
Crangon crangon	1				1	1	1	34
Nephtys species					3	2		6
Lanice conchilega			7					49
Pectinaria koreni			1					
Pomatoschistus minutus				75	27	38	28	
Clupeidae larvae						50		

In July *Schistomysis spiritus* is again prominent, with juvenile gobies still important. In August a drastic change occurs and radioles of *Lanice conchilega* and small postlarval *Crangon crangon* are the main sources of energy.

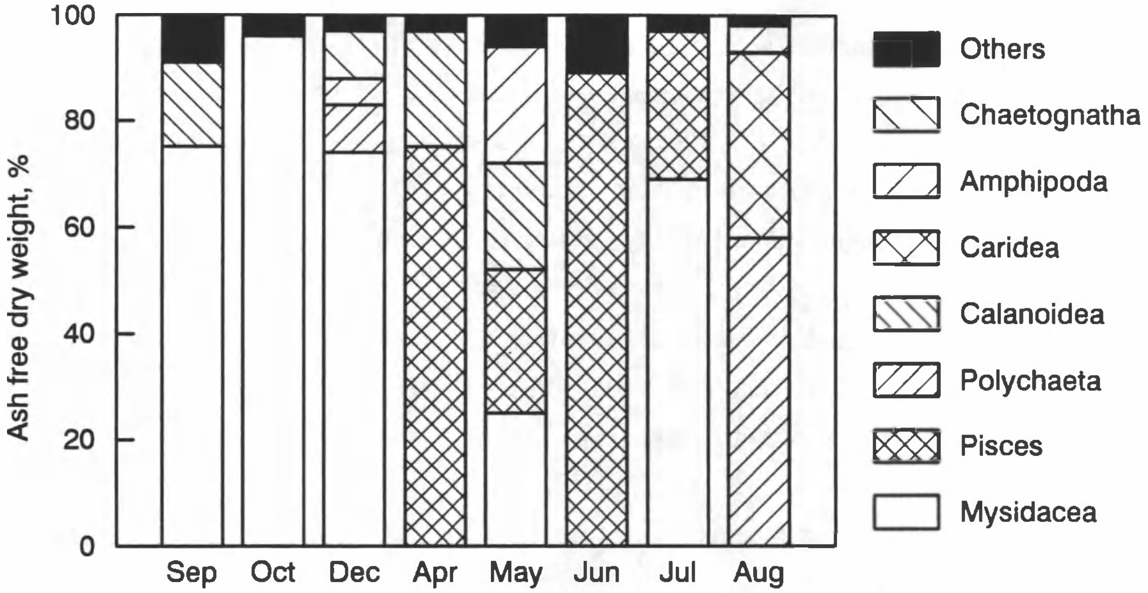


Fig. 5.2. Gravimetric food composition (%G as ADW) for *P. lozanoi* over the year.

Numerical food composition differs quite substantially from the gravimetric results (Table 5.1, Fig. 5.3). Here *Temora longicornis* gradually decreases in importance from September to December, replaced first by mysids and then by amphipods, 60% gammaridean, mainly *Microprotopus maculatus* and 40% caprellids: *Pariambus typicus*.

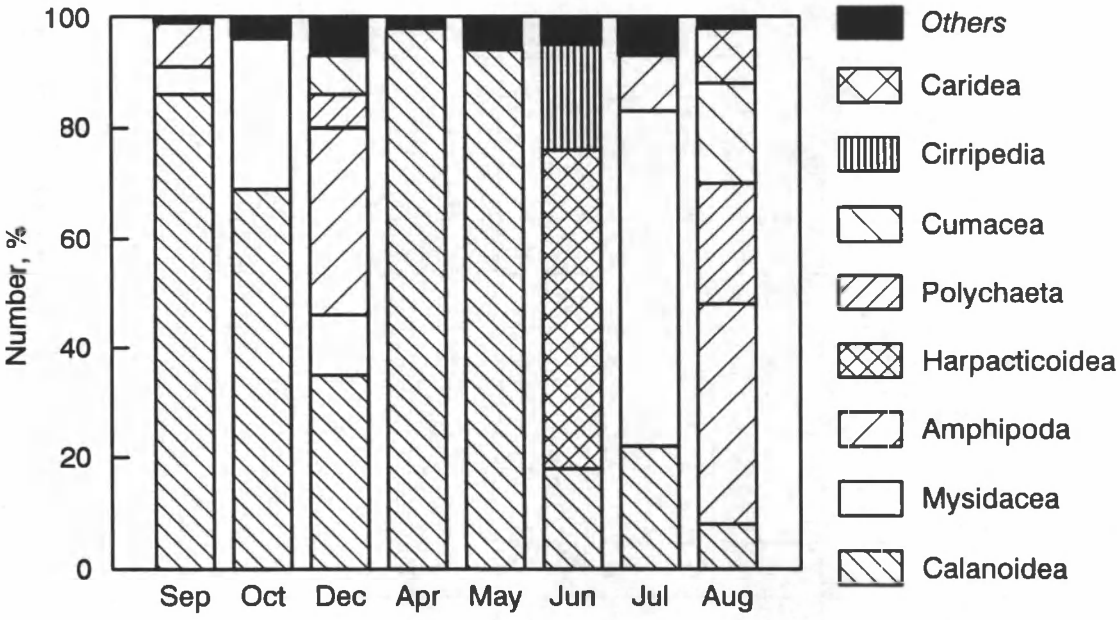


Fig. 5.3. Numerical food composition (%N) for *P. lozanoi* over the year.

In April and May *Temora longicornis* is extremely dominant, to be replaced by other calanoids, mainly *Centropages* species, harpacticoids, mainly *Microarthridion liitorale* and cypris larvae of Cirripedia in June. In July small mysids figure prominently. In August the picture is quite diverse with grossly equal proportions of gammaridean amphipods, mainly *Microprotopus maculatus*, caprellids: *Pariambus typicus*, sedentary polychaetes: *Lanice conchilega*, cumaceans, mainly *Pseudocuma longicornis* and some carideans, mostly *Crangon crangon*.

Only in September enough fish of 6 different size classes (from 25 to 55 mm) were collected within the same trawl to compare food consumption at different lengths. The numerical and gravimetric percentages of all species representing more than 4% in a single size class are shown in Table 5.2. The gravimetric composition is shown in Fig. 5.4.

Table 5.2. Number of stomachs examined, number of prey items and numerical and gravimetric food composition (main species) in different size classes of fish in September.

Fish size (mm)	25-30	30-35	35-40	40-45	45-50	50-55
Number of stomachs	4	13	30	30	24	9
Number of items	237	674	847	1188	1219	253
Prey species	Numerical percentage					
Temora longicornis	95	90	83	85	85	81
Schistomysis spiritus	1	3	6	5	5	6
Microprotopus maculatus	3	4	5	6	5	8
Prey species	Gravimetric percentage					
Temora longicornis	46	21	12	15	18	11
Schistomysis spiritus	51	75	80	74	73	68
Crangon crangon		1				11
Pomatoschistus species			4			
Diastylis species					5	

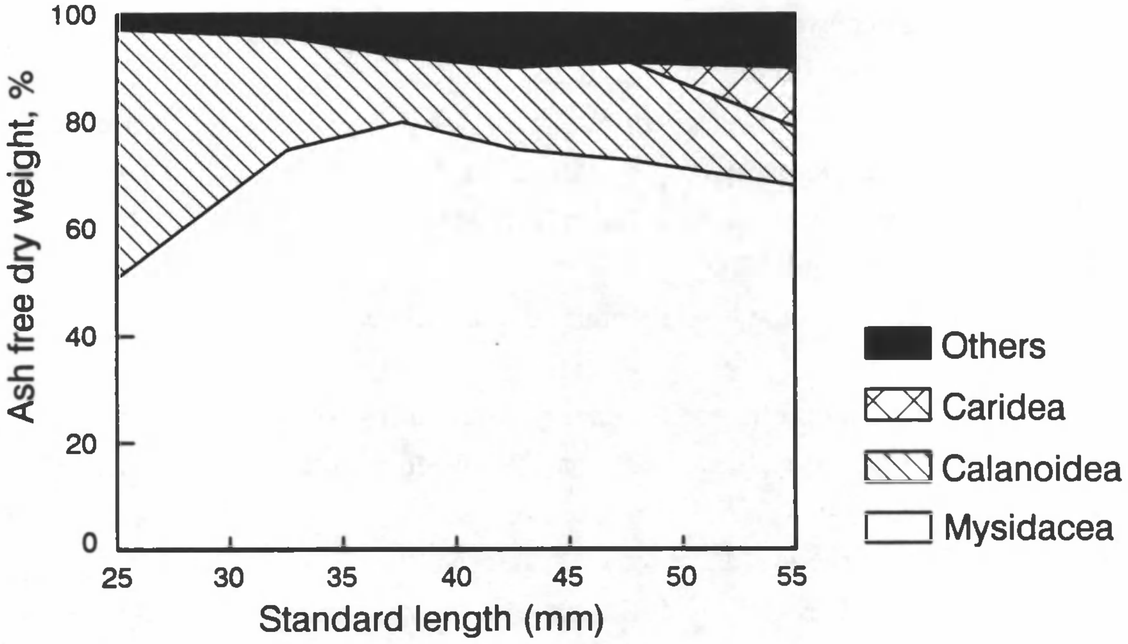


Fig 5.4. Gravimetric food composition of different size classes of *P. lozanoi* in September.

DISCUSSION

Stomach analysis data are commonly used for food web analysis. The results should be expressed in convertible units (Berg 1979). Most methods that pretend to quantify the energy pathways use gravimetric data based on weighing the stomach contents as present in the fish (Hyslop 1980). Our method of calculating the original AFDW has the advantage of reducing the bias introduced by the rapid digestion of soft bodied animals, e.g. chaetognaths.

The large differences between the numerical and the gravimetric percentage for many species points to a large size range in the prey consumed. One may wonder about the profitability of eating large numbers of *Microathridion littorale* if they contribute less than 1% to the total energy intake in the June sample.

In the shallow coastal zone *Pomatoschistus lozanoi* feeds predominantly on hyperbenthic animals, mainly *Schistomysis spiritus*, pelagic copepods, mainly *Temora longicornis* and juvenile gobies, mainly *Pomatoschistus minutus*. Thus the species must forage in the water column close to the bottom. This is similar to the feeding mode suggested for *Pomatoschistus norvegicus* (Gibson & Ezzi 1981). As most animals are found undamaged in the stomach, *Pomatoschistus lozanoi* clearly prefers suction feeding to biting, allthough the August result shows it to be perfectly capable of biting off the radioles of *Lanice*, just like *P. minutus* (Hamerlynck *et al.* 1986). Thus the restricted feeding mode of *Pomatoschistus lozanoi* is probably not due to anatomical constraints. The food resource partitioning with *Pomatoschistus minutus* may be a behavioural response to avoid competition.

Unlike *Pomatoschistus minutus* there is very little tendency towards more benthic feeding at larger sizes. Progenesis is common in the family Gobiidae (Miller 1984) and in a sense the feeding of the adult *Pomatoschistus lozanoi* can be seen as a progenetic character: juvenile *P. minutus*, and most other juvenile gobies feed to a large extent on pelagic and hyperbenthic animals (Lebour 1920, O. Hamerlynck unpubl. data).

A substantial proportion of the energy required for the ripening of the gonads in spring is obtained through predation on the juveniles of its possible competitor, *Pomatoschistus minutus*. Thus losing the competition for spawning sites, due to smaller size of the male, may have some advantages.

The northward extension of *Pomatoschistus lozanoi* may be limited by the total duration of the breeding season for both species taken together. At a certain latitude the season may become to short for *P. lozanoi* juveniles to profit from the autumn copepod and mysid bloom.

In view of the resource partitioning between *Pomatoschistus minutus* and *P. lozanoi*, putting them in a single "sand gobies" category may lead to incorrect conclusions in ecological studies. In general, taxonomic lumping leads to greater errors than establishing functional guilds (Sugihara *et al.* 1986). In a functional guild analysis of the inshore fish community, lumping according to similar size and food, *Pomatoschistus lozanoi* would be probably be grouped with juvenile herring and sprat rather than with *P. minutus*. When calculating fluxes to and from the gobies in a coastal area this must be taken into account. The results of Doornbos & Twisk (1987) for the saline Lake Grevelingen will be more or less valid as *P. lozanoi* is only common in the westernmost part of the Lake (O. Hamerlynck unpubl. data). The spring data of Boddeke *et al.* (1986) for the Dutch coastal area almost certainly concern *P. lozanoi* and not *P. minutus* that has a very low catchability at the time of spawning (Hamerlynck *et al.* 1986). When calculating fluxes to gadoids (Redant 1977), *Trachinus vipera* (Creutzberg & Witte 1989) and other fish that consume large quantities of gobies, identifying the species seems important: the energy derived from *P. lozanoi* comes from secondary and tertiary production in the water column rather than indirectly through the benthic component as in *P. minutus*.

ACKNOWLEDGEMENTS

We thank Luk Bogaert for hospitality on board the O62, and Dr. F. Redant of the FRI, Ostend for some of the samples. This research was supported by the Concerted Actions Oceanography of the Ministry of Scientific policy.

Chapter 6

Daily ration of juvenile *Pomatoschistus lozanoi* de Buen (Pisces: Gobiidae). Influence of circadian, circatidal and semilunar rhythms

Hamerlynck, O., Cattrijsse, A. & Arellano, R.V. (submitted a). Daily ration of juvenile *Pomatoschistus lozanoi* de Buen (Pisces: Gobiidae). The influence of circadian, circatidal and semilunar rhythms.

ABSTRACT

In order to estimate daily ration of juvenile *Pomatoschistus lozanoi* and to evaluate the effect of tide and daylight on its feeding activity, two 24 hour samplings were performed, one (in 1985) with high water around midnight, the other (in 1986) with low water around midnight. Incidently the sampling in 1985 was around neap tide and in 1986 it was around spring tide. The fish were observed to feed more intensively during the night. Daily ration in 1985 was estimated to be about 1 % of body Ashfree Dry Weight (ADW). For 1986 the estimate is about 5 % of body ADW in spite of similar water temperatures at both sampling dates. It is suggested that a semilunar rhythm, either in the fish or in the invertebrate prey, is the basis of the observed difference. This phenomenon may also explain the prominent 14-ring bands observed in the otoliths. Because of the influence of the various rhythms on feeding activity in fishes living in a strongly tidal environment, an accurate estimate of daily ration from production estimates and a P:C ratio established in the laboratory may be logistically less demanding than an estimate from stomach content data.

INTRODUCTION

Daily ration, the amount of food consumed by an animal over 24 hours, is a basic parameter in the study of the trophodynamics of ecosystems. With the development of multispecies models of fisheries management, this parameter has taken on increased importance also in the field of applied ecology (Sissenwine &

Daan 1991).

In field studies of fish, daily ration can be determined by assessing stomach content at regular intervals over a 24 hour period and then, with the knowledge of a rate of gastric evacuation, calculating total consumption over the period considered.

A wide variety of models exists, both for the determination of the rate of gastric evacuation and for the calculation of consumption. The literature on gastric evacuation models is full of heated debate (e.g. Jobling 1986, Olson & Mullen 1986) on the respective merits and shortcomings of the various models but in most circumstances the results of the different models are virtually indistinguishable. The exponential model of gastric evacuation is both adequate and convenient because of its simplicity (Persson 1986). The most widely used consumption models, namely the Eggers (1977) model and the first model of Elliott & Persson (1978), assume an exponential rate of gastric evacuation (see also Cochran 1979, Eggers 1979, Elliott 1979). Until recently it was assumed that the Eggers model, which is much simpler, required stomach contents to be equal at the beginning and the end of the 24 hour period. However, Boisclair & Leggett (1988) have shown the Eggers model to be quite robust: even when the assumptions are violated the estimate of daily ration is accurate. Some models do not require an independent estimate of the rate of gastric evacuation (Sainsbury 1986, Jarre *et al.* 1991). However, an abrupt transition between the feeding periods and the nonfeeding periods is needed for an estimate of this rate from field data.

In most fish activity is clearly synchronised with the light-dark cycle but in the sea there is an additional tidal stimulus (Gibson 1993). Most often there is a correlation between activity and feeding but the physiological basis of these rhythms is still poorly understood (Boujard & Leatherland 1992). The documentation and understanding of these rhythms is also important for aquaculture (Parker 1984), i.e. feeding the fish at the wrong time will result in poor growth performance.

Sand gobies of the genus *Pomatoschistus* are the most abundant fish in shallow coastal areas and estuaries of the North Sea (Hamerlynck *et al.* in press) and, like other small gobiids, are important prey for 0-group gadoids (Fosså 1991, Hamerlynck & Hostens 1993). *Pomatoschistus lozanoi* is known to feed mainly on hyperbenthic mysids (Hamerlynck *et al.* 1990). No studies have so far addressed the feeding rhythm of *Pomatoschistus lozanoi*. It is known that the closely related and sympatrically occurring *Pomatoschistus minutus* is mostly active during the night (Berge *et al.* 1983). However, in a tideless environment Evans (1984) could not detect any diurnal rhythm in feeding activity. According to Gibson & Hesthagen (1981) in constant conditions *P. minutus* has an endogenous circatidal rhythm with peak activity around low tide. In normal light-dark conditions this activity is greatly enhanced at night. In the Ythan estuary Healey (1971) observed peak feeding by *P. minutus* at high tide.

On the basis of two 24 hour cycles using *Pomatoschistus lozanoi* of 25-30 mm standard length the existence of a feeding rhythm is assessed, daily ration is calculated using different models and, the nature of the rhythm found is tentatively defined.

MATERIALS AND METHODS

Study area

The study site is an exposed sandy beach close to the mouth of a tidal creek which is the entry to a 125 hectare saltmarsh: the Zwin nature reserve.

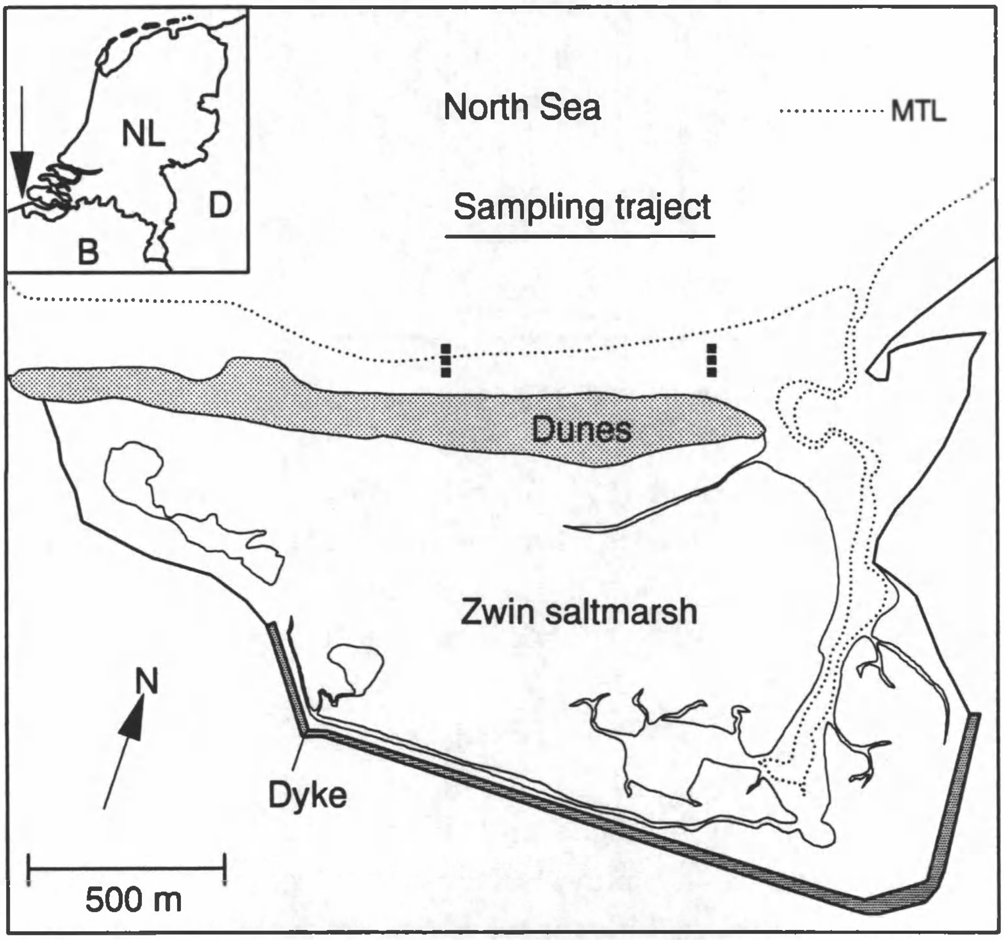


Fig. 6.1. Map of the study area with the sampling traject. MTL is the mean tidal level as defined for Amsterdam. Inset: position of the study area in relation to the Netherlands (NL), Belgium (B) and Germany (D).

This reserve is situated at the mouth of the Westerschelde estuary, the southernmost estuary of the Dutch Delta, near to the Dutch-Belgian border (Fig. 6.1). The fish and epibenthic invertebrate community of the Delta is described in Hamerlynck *et al.* (in press). Salinity at the sampling site varies between 27 and 32 ppt. Average tidal amplitude is 429 cm at spring tide and 283 cm at neap tide (total average 368 cm) (Fig. 6.2).

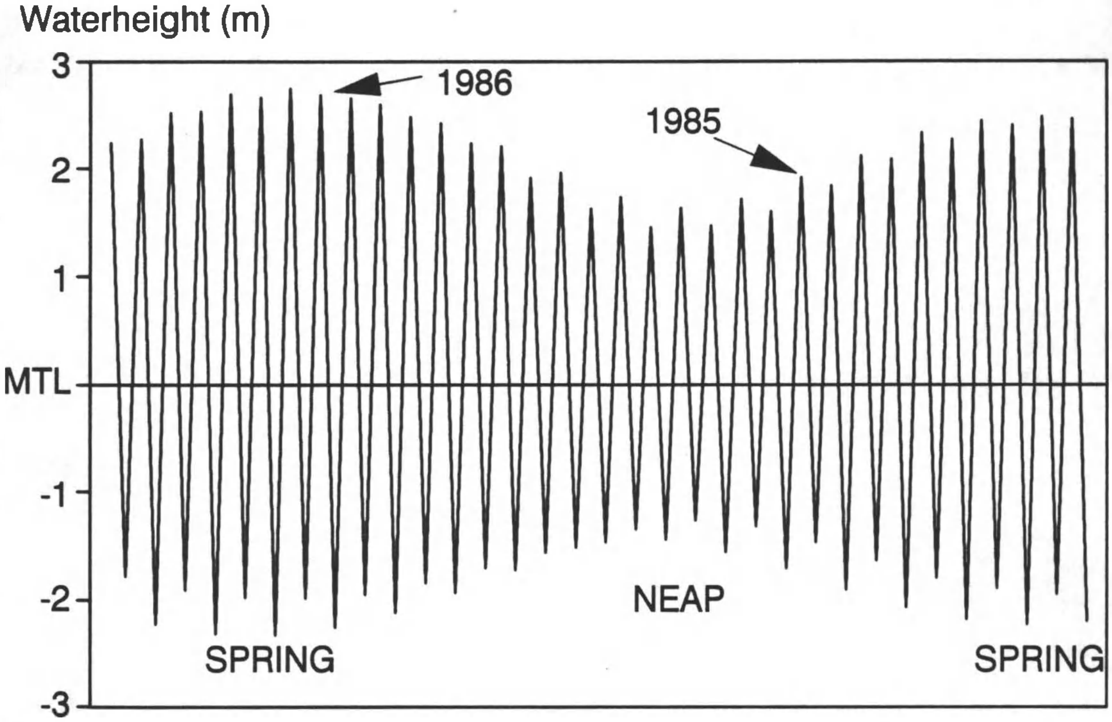


Fig. 6.2. Typical spring-neap tidal cycle at the sampling site with the position of the 1985 and 1986 samplings in relation to the spring-neap cycle.

Tidal currents are longshore (SW-NE) with maximal velocities of 1.7 ms^{-1} about 1 hour before high and low water. Median grain size of the sand fraction at 6 m below Mean Tidal Level (MTL) is 171 μm, mud content is on average 4.7 %. Some *Lanice conchilega* beds are found close to the sampling site.

Sampling

Samples were taken from a small vessel in the shallow subtidal of a sandy beach using a two-metre beam trawl (Kuipers 1975) equipped with a 5x5 mm mesh net. Hauls were taken parallel to the beach at 6m below MTL. Haul length, between two sets of radar beacons set on the beach, was approximately 700 m. Haul duration varied depending on current velocities but was 13 minutes on average (minimum 7, maximum 26 minutes). Depending on the number of fish caught 2 to 4 hauls were taken for each time interval. All fishes caught were anaesthetised in a Benzocaine solution in sea water to avoid unnecessary suffering and to prevent regurgitation of stomach contents and then preserved in neutralised formaldehyde in sea water (10 % final concentration). Data on the variation in catch rates of gobies and other fish will be reported elsewhere.

In the laboratory between 13 and 20 *Pomatoschistus lozanoi* of between 25 and 30 mm standard length (SL) were selected at random, preferably from a single haul, for stomach analysis. The midpoint between the start and the end of that haul (or occasionally of a set of hauls) is taken as the time of the sample. All prey items encountered were identified, if possible to species level. In the present study only the numerically dominant prey types (occurring on average with over 1 item per stomach): two groups of Copepoda, namely harpacticoids and calanoids and two larval stages of Cirripedia, namely nauplii and cypris larvae are discussed. The original ash free dry weight (ADW) of the prey items prior to digestion was calculated from regressions established for the same general area (Appendix). Stomach contents were weighed on a Mettler M3 microbalance (accuracy 1μg) after drying for two hours at 110 °C and expressed as Fullness Index (FI):

$$FI= \frac{S_i}{W_i} * 100$$

with S_i the dry weight of the stomach content in mg and W_i the Ashfree Dry Weight (ADW) of the fish in mg. Fish ADW were taken from a length-ADW regression (Hamerlynck *et al.* 1986). Prior to use of FI data in consumption models or statistical tests these were arc sin transformed for normalisation and backtransformed when mean FI's were needed (Sokal & Rohlf 1981).

In 1985 sampling was started at 14:58 Central European Time (CET) on 25 September (tidal amplitude about 360 cm, high tide at midnight). Twelve approximately two-hourly samples H1 to H12 (average interval 172 minutes) were taken and sampling was concluded at 15:02 CET the next day. Sea water temperature was 17.5 °C. Because of low catches during the day most stomach content data are a mixture of two consecutive hauls. H2 and H9 are mixtures 4 consecutive hauls.

In 1986 sampling was begun at 9:30 CET on 11 August (tidal amplitude just over 4 m, low tide at midnight). Fourteen samples H1 to H14 (average interval 106 minutes) were taken and sampling was concluded at 10:25 CET the next day. Sea water temperature was 18 °C. Because of the high number of gobies caught all stomach content data refer to single hauls.

As, for a specific locality, the time of day of a certain semilunar tidal phase, e.g. spring tide high water is constant, the deliberate choice of comparing a high water midnight with a low water midnight sampling, resulted in the 1985 and 1986 samplings to be at contrasting periods of the spring-neap cycle (Fig. 6.2).

To assess if a feeding rhythm was present, two consecutive minima and the intermediate maximum within each 24 hour cycle were tested using a pairwise multiple comparison among means (Sokal & Rohlf 1981). Because of the range of sample sizes (13 to 20 stomachs analysed per time interval) in 1985 the GT2 method was used. For the 1986 data (19 or 20 stomachs analysed per time interval) the more powerful T'-method could be used. In view of the small size interval of the fishes examined it was unnecessary and impracticable to use ANCOVA (Jenkins & Green 1977, Fernandez *et al.* in press) to adjust for size differences among the fishes.

Calculation of daily ration

Several approaches were followed in order to estimate the daily ration from the 24-hour sampling. In the different models the terminology of Jarre *et al.* (1991) is followed throughout.

For use in the Eggers (1977) and Elliott & Persson (1978) models the instantaneous rate of gastric evacuation E as determined by Andersen (1984) for *Pomatoschistus microps* was used:

$$E = 7.385 \times TL^{-0.832} \times e^{0.0639(T-20)}$$

where TL is the total length of the fish, which equals 1.089 + 1.157 x standard length (SL) (Hamerlynck *et al.* 1986) and T is the ambient temperature.

According to the Eggers (1977) model daily ration R_d is determined as:

$$R_d = \overline{FI} \times E \times 24$$

where $\overline{FI}$ is the average fullness index of all fish collected.

The Elliott & Persson (1978) model states that:

$$R_d = \sum_{\Delta t=1}^{p} \overline{J_{\Delta t}}$$

where $\overline{J}_{\Delta t}$ is the quantity of food consumed during an interval Δt between two successive sampling periods t and $t+1$ and p is the number of such intervals per day. $\overline{J}_{\Delta t}$ is defined as:

$$\overline{J_{\Delta t}} = \frac{(\overline{FI_{t+1}} - \overline{FI_t}\, e^{-ET})\ E\ T}{(1-e^{-ET})}$$

where $\overline{FI}_t$ and $\overline{FI}_{t+1}$ are the mean fullness indices at two successive sampling periods and T is the time between two successive sampling.

The first model of Sainsbury (1986) was slightly adapted and applied to the data using the NONLIN option in SYSTAT for parameter estimation. According to this model R_{cd}, the food consumed during time interval cd is

$$R_{cd} = \int_{t=F_b}^{t=F_s} J\, dt = J\ (F_s - F_b)$$

where cd is the duration of a complete feeding cycle, F_b is the moment at which the fish begin to feed and F_s is the moment at which the fish stop feeding. In Sainsbury's original model cd was set equal to 24 hours, but in the present study feeding cycles were clearly shorter than 24 hours. We have therefore preferred to define cd as the time between two successive minima in the stomach fullness trajectory, i.e. 17 hours 42 minutes for the 1985 data and 14 hours 25 minutes for the 1986 data. Assuming the cycles before and after the modelled time interval are of similar duration and intensity, consumption over 24 hours can be calculated as:

$$R_d = \frac{R_{cd}}{cd}\ x\ 24$$

The time trajectory of stomach fullness in the model has two different forms: when feeding

$$FI_t = \frac{J}{E} + (FI_{F_b} - \frac{J}{E})\ e^{-E(t-F_b)}$$

and when not feeding

$$FI_t = FI_{F_s}\ e^{-E(t-F_s)}$$

F_b, F_s, J and E are the four parameters estimated by the model. The two remaining quantities namely FI_{Fb} and FI_{Fs} are defined in term of the parameters as follows:

$$FI_{F_b} = \frac{J}{E} \times \frac{(e^{-E*(cd-(F_s-F_b))} - e^{-cd*E})}{(1 - e^{-cd*E})}$$

and

$$FI_{F_s} = \frac{J}{E} + (FI_{F_b} - \frac{J}{E})$$

For the 1986 data the fit between the model and the data in the time trajectory between the supposed end of feeding activity and the start of the next feeding cycle was poor. Therefore the gastric evacuation rate *E*, as estimated by the model from the 1985 data was used as a constraining variable in the model for the 1986 data and only three parameters were estimated.

For the interpretation of the feeding rhythms found, thin slices of goby otoliths, collected in a comparable shallow coastal area 50 km north of the study site were studied. In the goby otoliths a clear banding pattern can be observed and each band consists of 14 rings (Arellano, unpublished) .

RESULTS

In both years the fish exhibit strongly fluctuating stomach fullness with high individual variability (Fig. 6.3). In 1985 (Fig. 6.3a) highest FI was found in the first haul. Next, mean FI followed tidal height of a first tidal cycle quite closely with a peak a few hours after midnight. During the next (daytime) tidal cycle feeding activity was low, with a slight increase in variability of stomach content at the end of the investigated time period. In 1986 (Fig. 6.3b) mean FI is decreasing during the first three hauls, then there is a small peak with high variability in H4. Next, mean FI increases steadily until about midnight corresponding to the low tide. Then stomach fullness decreases again until dawn, with possibly a new feeding cycle starting towards the end of the investigated time period.

There are significant differences between two consecutive minima and the intermediate maximum FI in both years (Table 6.1) indicating that a rhythm is present ($p < 0.01$ for all comparisons).

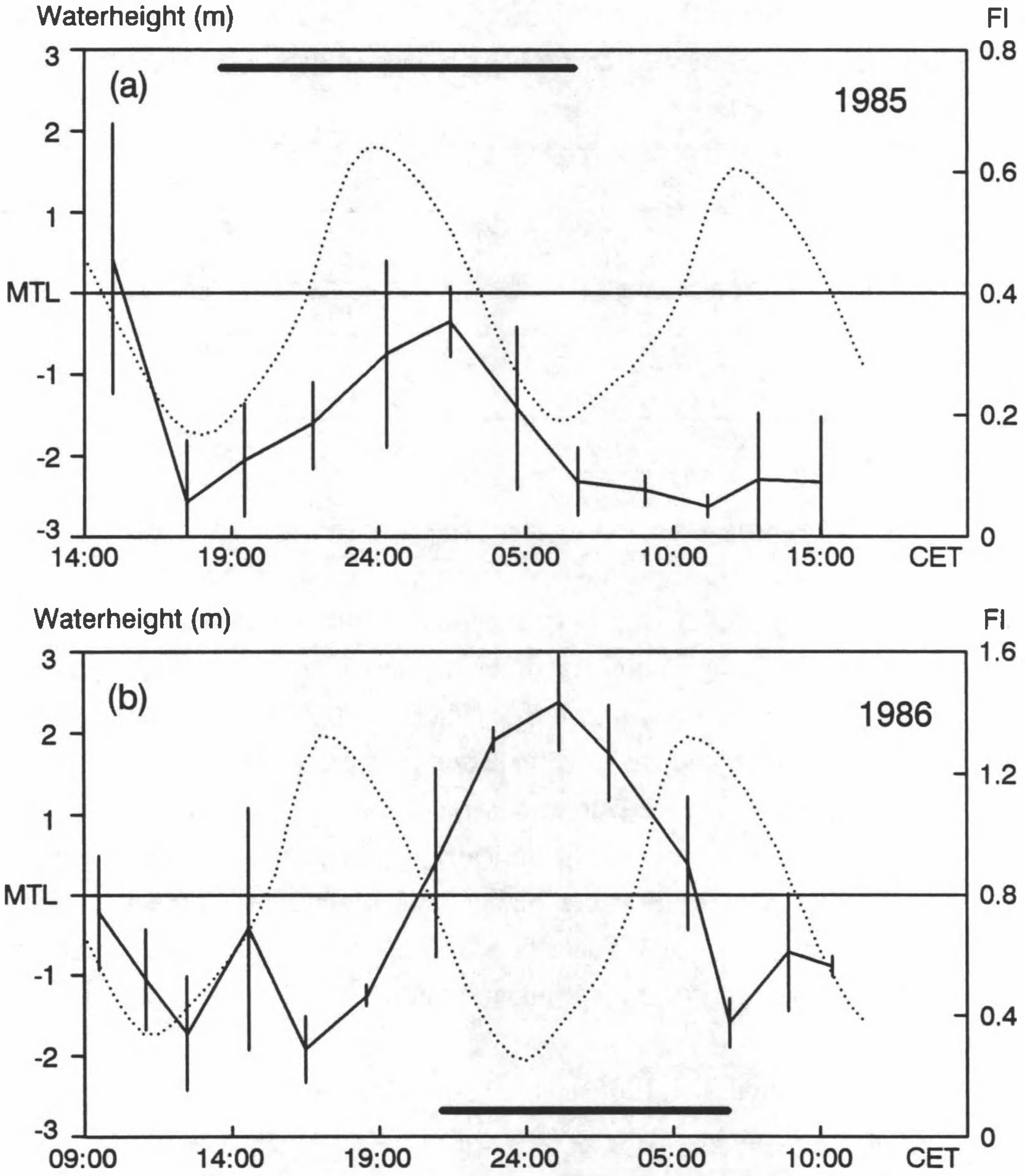


Fig. 6.3. Time trajectories of mean stomach fullness (FI, backtransformed arc sin transformed) with standard deviation (full line, right scale), and water height (dotted line, left scale) for 1985 (a) and 1986 (b). The dark bar represents darkness.

The daily ration as a percentage of body weight, calculated according to the different models, is tabulated in Table 6.2. Daily ration in 1986 is at least four times higher than in 1985 for each of the models used. Fig. 6.4 shows the result of the Sainsbury model simulation. The gastric evacuation rate *E*, as estimated from the 1985 data (0.211) is lower than that estimated from the Andersen (1984) formula (0.35 for 1985 and 0.36 for 1986) used in the Eggers (1977) and the Elliott & Persson (1978) models.

Table 6.1. Pairwise multiple comparison of two consecutive minima and the intermediate maximum (arc sin transformed) fullness indices (k = number of pairs, v = degrees of freedom).

1985 GT2 method (k = 3; v = 50) critical value for p < 0.01 = 3.087		
Hauls	H2	H10
H6	4.297	5.073
1986 T' method (k = 3; v = 56) critical value for p < 0.01 = 4.301		
Hauls	H5	H12
H9	8.466	7.682

Qualitatively the 1985 feeding peak at high tide corresponds to an increased intake of nauplii (Fig. 6.4a). Afterwards cypris larvae and calanoids become more important. In 1986 average numbers of cypris larvae and calanoids found in the stomachs are much higher than in 1985 (Fig. 6.4b). The time trajectory of the number of cypris larvae and, to a lesser extent, harpacticoids (Fig. 6.4c) found in the stomachs corresponds to the pattern observed in the fullness indices. It should be noted that in gravimetric terms the numerically dominant prey items were relatively unimportant. Differences in FI were mainly due to rare but large items such as shrimp larvae, mysids and small fishes but these are to rare to show any meaningful time trajectory numerically (Cattrijsse unpublished).

Table 6.2. Daily ration for 1985 and 1986, expressed as % of body ADW, as estimated from the different models.

MODEL	1985	1986
Eggers	1.183	5.384
Elliott & Persson	1.044	5.886
Sainsbury	0.906	4.585

DISCUSSION

Juvenile *P. lozanoi* fed more intensively at night than during the day in both years. This result seems to confirm the observations in the closely related *P. minutus* (Gibson & Hesthagen 1981, Berge *et al.* 1983).

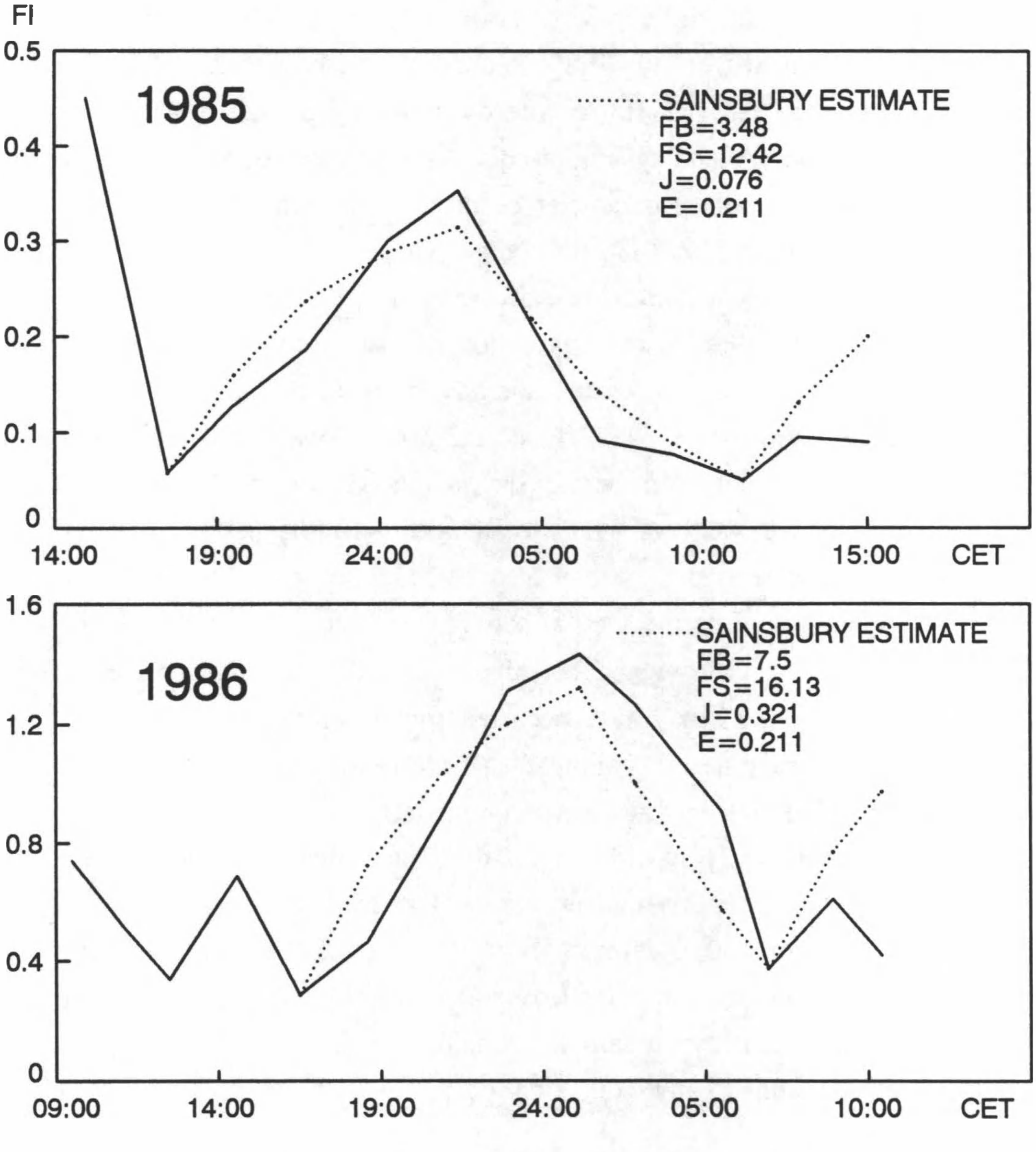


Fig. 6.4. Time trajectories of measured stomach fullness (FI, full line) and as estimated from the Sainsbury (1986) model (dotted line) for 1985 (a) and 1986 (b). FB is the moment at which the fish begin to feed (relative to origin, i.e. 14:00 hours Central European Time (CET) for 1985), FS is the moment at which the fish stop feeding, J is ingestion rate and E is the gastric evacuation rate.

The obvious explanation for feeding under the cover of darkness would be predator avoidance: Magnhagen (1988) observed a decrease in feeding activity of *P. minutus* in the presence of cod. In highly turbid estuarine areas avoidance of visual predators may be less important and the flood tide linked activity observed by Healey (1971) may be primarily related to the exploitation of the food-rich intertidal areas.

The different models used for the estimation of daily ration all gave comparable results. The estimates of the Sainsbury (1986) model were lower than in the Eggers (1977) and Elliott & Persson (1978) models because the gastric evacuation rate derived from the 1985 field data was lower than that established for *P. microps* by Andersen (1984). As already stated by Sainsbury (1986) his model requires quite an abrupt and synchronised transition from feeding to non-feeding in the whole population for the parameter estimates to be reliable. In 1985 this seems to have been the case but in 1986 the 'bulge' on the descending arm of the feeding trajectory precluded unconstrained use of the model. However, the fit of the model as constrained by the 1985 gastric evacuation estimate seems acceptable (Fig. 6.4b). From Fig. 6.4 it can also be seen that the adaptation of the model to a shorter time interval than 24 hours has probably biased the result. Indeed in 1985 (Fig. 6.4a) the highest fullness was achieved before the simulated period started and the next feeding cycle, if there was one, seems to have started rather less intensively than the modelled one. This second bias may also be valid for the 1986 data (Fig. 6.4b). Here the modelled time period may also have been set a little too short because of the aberrant result of H4, which contained two outliers with high FI. The true (population) minimum FI may have occurred somewhat earlier and the slope of the ascending arm of the trajectory would then have been somewhat lower. Jarre *et al.* (1991) developed a model that can accommodate two feeding periods within 24 hours and that potentially would use all the data instead of only the time period between two successive minima. However, though Jarre *et al.* (1991) applied it to a 24 hour data set for cod (Arntz 1974) it is our contention that, for an accurate estimate, the data should then extend over at least two complete feeding cycles and that the time interval between samples should even be shorter than in the present study. Otherwise almost any collection of points can be accommodated by the model.

Unfortunately we have not been able to provide confidence intervals for the different models. The statistical treatment of daily ration estimates is not simple. Elaborate techniques have been proposed by Worobec (1984) but not all sources of variance can be estimated separately. The Sainsbury model as used in SYSTAT gave a measure of fit (r^2 of 0.82 and 0.93 for 1985 and 1986 respectively) but, as only the averages were used, only part of the total variance was accommodated. The bootstrap technique applied to daily ration estimates by Boisclair & Leggett (1986) seems adequate but is not widely available.

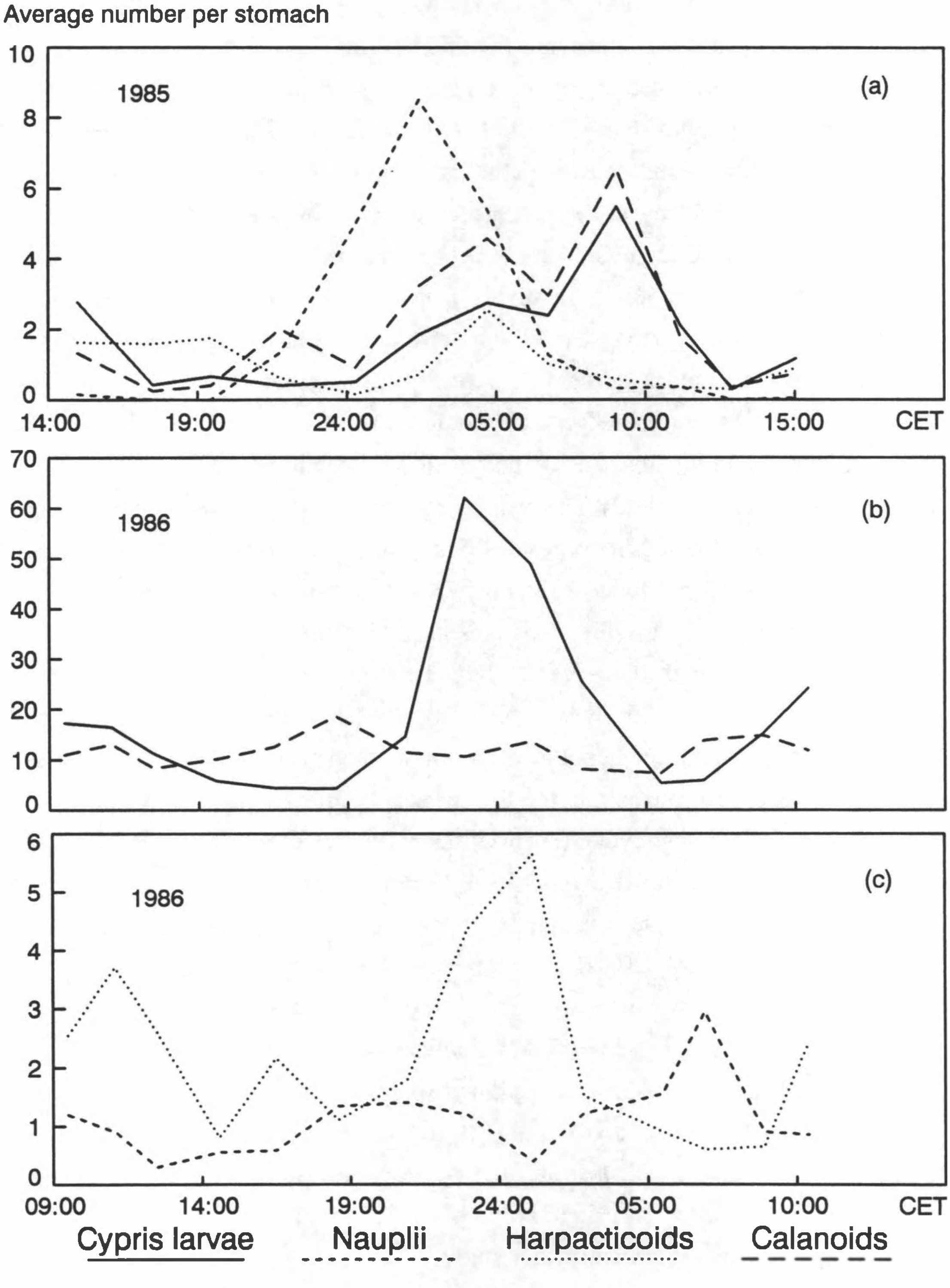


Fig. 6.5. Time trajectories for the average number of items per stomach of the numerically dominant food categories (a, 1985, b and c, 1986).

Whatever the true daily ration may have been in either year it was clearly at least four times lower in 1985 than in 1986 and this requires an explanation. Many different hypotheses, that can not be falsified on the basis of the present field results, where many biotic and abiotic factors known and unknown may influence feeding intensity, can be proposed to account for this finding.

Part of the explanation for the higher daily ration in 1986 may be the effect of daylength on growth rate. Fonds (1979) observed that growth rate and food consumption in plaice and sole, kept in the laboratory at constant temperatures but with a natural daylight cycle, were correlated to daylength, thus being maximal in June and minimal in December. However, between early August and late September this would only account for a relatively small difference in feeding intensity. For example, in *P. microps* from a tideless environment Antholz *et al.* (1991) observed little difference in stomach fullness between July and September.

Evans (1984) measured a daily ration of 5-12 % of body dry weight for *Pomatoschistus minutus* and 1% of body ADW consumption as estimated for 1985 seems to be a very low daily ration for fast growing tiny fishes. Therefore gobies were possibly food limited in August 1985 and not in September 1986. Without data on the time trajectory of food availability in the area it is impossible to verify this. From the stomach analyses (Fig. 6.5) it is clear that the items taken most frequently were largely the same in both years. Only the cypris larvae of Cirripedia showed a similar time trajectory in both years, being mostly taken around low tide.

The food limitation hypothesis is not incompatible with the hypothesis that feeding intensity was related to the spring-neap cycle as prey abundance may be determined by the same cycle (e.g. Morgan 1990). There is an ovious selective advantage for barnacle larvae, which have to settle in the upper part of the intertidal zone, to make use of the spring-neap cycle. The observation that goby otoliths collected from a shallow coastal area can exhibit a strongly banded pattern with 14-rings within each band suggests that a semilunar rhythm in growth and food consumption may be present (R.V. Arellano unpubl. data). However, though preliminary counts in relation to the known spawning time of *P. lozanoi* suggest the rings are daily (R.V. Arellano unpubl. data), validation of the daily nature of the rings has yet to be accomplished and the possible correspondence to the spring-neap cycle, i.e. wider rings deposited around spring tide and thinner rings deposited around neap tide, also requires further study.

CONCLUSIONS

From the present study it is clear that using an estimate of daily ration from a single 24-hour cycle to calculate food consumption by fishes living in a tidal environment may lead to considerable over- or underestimates of consumption when extrapolated over longer time periods.

Estimates of daily ration in fish can be made, either from the (instantaneous) rate of passage of food through the gut or from growth measurements (Wootton 1990). In the field the first method requires measurements of stomach fullness made at regular intervals over a 24-hour period as was done in the present study. For the second method field measurements of growth and mortality have to be done over a longer time interval e.g. one month. It is then possible to calculate production over that interval (Crisp 1984) and, with the use of a production:consumption (P:C) ratio, to estimate the consumption needed to achieve that production (e.g. Hamerlynck & Hostens 1993). Both methods are logistically demanding and labour intensive and most often some laboratory measurements of essential parameters have to be accomplished. The results of the present study suggest that for fishes in tidal environments the second method may be more rewarding in view of the high variability in daily ration found. However, if the correlation between daily ration and the spring-neap cycle can be substantiated it may be possible to derive a simple function describing its variation over time.

The large difference in daily rations established for both sampling dates cannot be explained by temperature differences, nor by the different time of the year. A range of other factors may have contributed to the result but the hypothesis advanced in this study is that daily ration and growth of gobies, and perhaps of other fishes in tidal areas, is to a large extent determined by the phase of the tide i.e. exhibits a semilunar rhythm. A semilunar rhythm is expected in benthic feeding animals such as plaice (R.N. Gibson pers. comm.) that exploit the richness of intertidal flats during high tide or in fishes that are exclusively intertidal (e.g. Northcott 1991). Its significance is rather less obvious in zooplankton feeding subtidal fishes such as the 25-29 mm *P. lozanoi* in the present study. In the field it is impossible to distinguish between endogenous and exogenous rhythms and the hypothesis that the semilunar pattern in feeding activity, tentatively derived from the present study, is entrained by semilunar rhythms of prey activity can not be discarded.

ACKNOWLEDGEMENTS

Without the enthusiastic logistic support of Rijkswaterstaat, meetdienst Vlissingen and especially of J. Gossé, C. Scheers, and skipper W. Goedegebuure this study could not have come into being. Gratitude is also extended to all students, marine biologists on the dole, friends and relations that volunteered to suffer with us during sampling. The second author acknowledges a grant from the IWONL, the third author acknowledges a grant from the Belgian Administration for Development Cooperation (ABOS). Dr. P.M.J. Herman pointed our attention to the possibility of simulating discontinuous functions in SYSTAT. This research was supported by Belgian FKFO grant 21.0094.92.

Chapter 7

Mesacanthion diplechma (Nematoda: Thoracostomopsidae), a link to higher trophic levels?

Hamerlynck, O. & Vanreusel, A. (in press). *Mesacanthion diplechma* (Nematoda: Thoracostomopsidae), a link to higher trophic levels? Journal of the marine biological Association of the United Kingdom.

ABSTRACT

The nematode *Mesacanthion diplechma* Southern is relatively rare in sediments of the Southern Bight of the North Sea and the Dutch Delta. Strangely, it is about the only free-living nematode found in the stomachs of the sand goby *Pomatoschistus minutus* Pallas from the same general area and even more peculiarly several hundred animals were found in sand gobies from the central part of the Oosterschelde. The large size of the nematode and its preference for the superficial sediment layers are probable causes for the first observation. For the second observation there is at present no explanation that can be substantiated. Some nematodes are known to aggregate on dead animals and possibly the Oosterschelde gobies may have been feeding on such an aggregation.

INTRODUCTION

In a recent review on the importance of meiofauna as food for fish (Gee 1989) it is suggested that nematodes may be less important than other meiofaunal taxa, in spite of their numerical dominance in the sediment. In general it is assumed that nematodes play an important role in the recycling of nutrients through the benthos but that they do not directly contribute to the higher trophic levels of the marine food web (review in Heip *et al.* 1985).

In this study the species composition of the free-living nematodes recorded in the stomachs of *Pomatoschistus minutus* Pallas from the shallow coastal areas of the Southern Bight and the Dutch Delta is compared to their occurrence in meiofaunal samples from the same general area.

RESULTS

Mesacanthion diplechma Southern belongs to the family Thoracostomopsidae which is characterised by the presence of complex mandibular structures in the buccal cavity. The strong jaws suggest it is a predator/omnivore (Wieser 1953). *Mesacanthion* has a mandible structure similar to *Enoplolaimus*, which, according to Platt & Warwick (1983), are voracious predators, as several specimens were found ingesting other nematodes. *M. diplechma* is a large nematode with a body length of 3.3 to 4.2 mm, a diameter of 76 to 145 µm (Platt & Warwick 1983) and an average biomass (dry weight) of 10 µg for females and 4.5 µg for males. The species has an affinity for silty, fine sands (Vanreusel 1991) and according to Lorenzen (1974) reproduces once a year between April and July. It is a typically coastal species which will occur fairly consistently in stations with the right sediment but always in low numbers: less than 10 individuals per 10 cm² (Vincx 1986, Vanreusel 1991). This has to be compared with the average of 1100 nematodes per 10 cm² for the Southern Bight (Heip *et al.* 1990). In detailed studies from the area where gobies were collected for the study of stomach contents, the species was recorded in about half of the stations examined (Table 7.1). Average size of nematodes in these stations is between 1.0 and 1.5 mm, with *M. diplechma* being larger than any other species present (Vincx 1986).

Table 7.1. The occurrence of *Mesacanthion diplechma* in the benthic samples: the number of stations with *M. diplechma* (N_d), the total number of stations examined (N_s) and the total number (N_t) of individuals (I) found allocated into males (M), females (F) and juveniles (J) if such data were available.

Area	Source	N_d/N_s	N_t
Belgian coast	Vincx 1986	23/50	5M, 5F, 58J
Voordelta	Vanreusel 1990	11/20	47 I
Oosterschelde	Sharma 1985 Smol 1986	1/2 1/6	5 I 1 I

Pomatoschistus minutus is the most abundant fish in sandy shallow coastal areas of the Southern Bight. It is a versatile microcarnivore with small crustaceans featuring prominently in the diet (Hamerlynck *et al.* 1986).

In an extensive study on the food of this goby in the Belgian coastal area and the Voordelta only 34 free-living nematodes were recorded from 1074 fish stomachs, compared to nearly 700 harpacticoids and 2 ostracods (Table 7.2). However, more than 90 % of the nematodes recorded in the stomachs were *M. diplechma*.

Table 7.2. The occurrence of *Mesacanthion diplechma* in the stomach of *Pomatoschistus minutus*: the number of *Mesacanthion diplechma* (N_m), the total number of nematodes (N_n), the number of harpacticoids (N_h), the number of ostracods (N_o), the number of foraminiferans (N_f), the total number of items found in the stomachs (N_i) and the number of stomachs of *Pomatoschistus minutus* examined (N_s).

	N_m	N_n	N_h	N_o	N_f	N_i	N_s
Belgian coast	28	31	455	2	5	16120	745
Voordelta	3	3	243	0	0	2946	329
Oosterschelde	268	268	77	0	125	650	28

In a sample of 28 gobies collected in a 1000 m trawl, covering 2600 m^2 of ground, in the Oosterschelde on 30 October 1987, a total of 268 *M. diplechma* were recorded. Ten gobies had no nematodes in the stomach. Eight gobies had 1 *M. diplechma* in their stomach, 6 gobies had between 2 and 7 nematodes and 4 gobies had between 15 and 169 *M. diplechma* in their stomach. The size range of gobies caught was 39 to 53 mm standard length. One of the gobies had a virtually undigested goby of 25 mm standard length in its stomach. The stomach of that predated goby held another 3 *M. diplechma*. All the nematodes recorded in the stomachs were females and juveniles. Energetically the nematodes are relatively unimportant in the diet: they account for just under 5% of the stomach contents in gravimetric terms.

DISCUSSION

The meiofaunal samples and the fish stomachs were not collected simultaneously, nor in strictly the same localities. However, the meiofauna of the general area has been intensively studied in different seasons over many years and samples have never yielded high numbers of *M. diplechma* (Heip *et al.* 1990). Therefore, it is strange to find that *M. diplechma* is about the only free-living nematode found in the stomachs of the sand goby *P. minutus*, in spite of its low abundance in meiofauna samples from the same general area.

Several explanations are possible. First, the cuticula of this species may be more resistant to digestion than in other species of nematode. It is well known that nematodes are digested rapidly (Hofsten *et al.* 1983) and thus their importance may be underestimated when examining stomach contents. However, other enoplids with a similar cuticular structure, such as *Enoplolaimus propinquus*, *Enoploides labiatus* (Sharma 1985) and *E. spiculohamatus* (Vanreusel 1990) are much more abundant in the sediment of the area studied and are not found in goby stomachs.

As argued by Gee (1989), meiofaunal animals, likely to be predated by lie-in-wait predators such as *Pomatoschistus*, should be active on the sediment surface. In the area studied nematodes (over 80 % of meiofauna) are much more abundant than harpacticoid copepods (less than 10 % of meiofauna) (Heip *et al.* 1990). The preference of the gobies for harpacticoids is clear from their relative importance in the stomachs (Table 7.2). The greater mobility of harpacticoids, making them more conspicuous, is probably a major factor in their susceptability to predation (Nelson & Coull 1989). The large size of *M. diplechma* and, presumably, its activity on or close to the sediment surface may render it more vulnerable to predation than the other nematodes present.

To explain the observation in the Oosterschelde, where nematodes were consumed more often than harpacticoids (Table 7.2), and where there was clearly a selective predation on the species *M. diplechma*, another mechanism has to be invoked. Other gobioids have been found to consume nematodes in accordance to their abundance in the sediment, but these data refer to non-selective omnivorous species (Fitzhugh & Fleeger 1985, Onakedo 1992). It is known that some nematode species aggregate on dead animals, i.e. *Pontonema vulgare* (Lorenzen *et al.* 1987), *Sabatieria migrans* (Gerlach 1977) and *Monhystera disjuncta* Bastian (Ólafsson 1992). Swarms of gobies were observed close to the mass aggregations of *P. vulgare*, though they were never actually observed feeding on them (Lorenzen *et al.* 1987). Perhaps, *M. diplechma* can also form such aggregations and such an aggregation may have been exploited by the gobies.

Though *M. diplechma* is the nematode most frequently consumed by *P. minutus* its importance as a link from meiofauna to higher trophic levels seems anecdotal.

Chapter 8

The food of *Pomatoschistus minutus* (Pisces, Gobiidae) in the Belgian coastal waters, and a comparison with the food of its potential competitor *P. lozanoi*

Hamerlynck, O. & Cattrijsse, A. (submitted). The food of *Pomatoschistus minutus* (Pisces, Gobiidae) in the Belgian coastal waters, and a comparison with the food of its potential competitor *P. lozanoi*. Journal of Fish Biology.

ABSTRACT

Data are presented on the food and gonado-somatic index of *Pomatoschistus minutus* obtained from the bycatch of a commercial shrimp trawler. *P. minutus* had a diverse diet including zooplankton and hyperbenthos but mainly epibenthic and benthic animals. During the spawning season males consumed high numbers of *Pomatoschistus* eggs, presumably after aggressive take-overs of territories. The food of *P. minutus* is compared to the food of *P. lozanoi* of the same size classes obtained from the same hauls. In the absence of data on predator and prey abundance the discussion on possible interference competition between the two species remains largely speculative.

INTRODUCTION

Gobies of the *Pomatoschistus minutus* species complex (Webb 1980) are the most abundant fish of the shallow coastal areas, estuaries and marine bays of the Dutch Delta (Hamerlynck *et al.* in press). They are also dominant fish in other European estuarine areas (Costa 1986, Le Mao 1986, Claridge *et al.* 1986, Henderson 1989, Elliott & Taylor 1989), in the Wadden Sea (Tiews 1990), in coastal areas of the Baltic Sea (Thorman & Wiederholm 1986, Zander 1990) and the Kattegat-Skagerak (Evans 1983, Pihl 1985).

Early studies on the food of *Pomatoschistus minutus* Pallas include Scott (1902) and Lebour (1920). More recent studies include Kühl (1961), Macer (1967), Healey (1971), Hesthagen (1971), Fonds (1973), Lee (1975), Morawski (1978), Schmidt-Moser & Westphal (1981), Evans (1983), Thorman & Wiederholm (1983, 1984, 1986), Magnhagen (1985), Pihl (1985), Claridge *et al.* (1985), Le Mao (1986), Boddeke *et al.* (1986), Doornbos & Twisk (1987), Zander & Hagemann (1987), Zander (1990), Mehner (1992), Aarnio & Bonsdorff (1993) and Hamerlynck & Vanreusel (in press). However, except for the studies of Fonds (1973) and Claridge *et al.* (1985) and the studies from the Baltic, where the closely related and morphologically similar *Pomatoschistus lozanoi* de Buen (Hamerlynck 1990) does not occur (Miller 1986), several of the studies may actually be dealing with a mixture of the two species.

Pomatoschistus species feature prominently in the energy budget of 0-group gadoids (Costa 1988, Hamerlynck & Hostens 1993), *Gobius niger* Linnaeus (Costa 1988), *Ciliata mustela* Linnaeus (Costa 1988), *Alosa fallax* Lacépède (Assis *et al.* 1992), *Trigla lucerna* Linnaeus (Costa 1988), *Anguilla anguilla* Linnaeus (Costa *et al.* 1992), *Echiichthys vipera* Cuvier (Creutzberg & Witte 1989), juvenile *Scophthalmus rhombus* Linnaeus and *Scophthalmus maximus* Linnaeus (Braber & Groot 1973) and even of piscivorous birds (Doornbos 1984). Young harbour seals depend on *Pomatoschistus* shortly after weaning (Sievers 1989).

Pomatoschistus species are repeat spawners. The males establish territories, usually under bivalve shells, and guard and fan the eggs, deposited on the shell by one or several females, until hatching (Miller 1984). In the Southern Bight of the North Sea *Pomatoschistus minutus* eggs were found from late April to early June, *P. lozanoi* eggs from late May to mid August (Fonds 1973). Gobies mature in the next spring and very few post-spawning adults survive into a second breeding season (Fonds 1973).

In the present study the food of *P. minutus* is described and compared to the food of *P. lozanoi* from the same samples. *P. lozanoi* was found to feed predominantly on hyperbenthic animals, especially *Schistomysis spiritus*, pelagic copepods, mainly *Temora longicornis*, and juvenile *P. minutus* (Hamerlynck *et al.* 1990).

MATERIALS AND METHODS

Gobies were obtained more or less monthly from the by-catch of the commercial shrimp trawler "O62" operating in the Westdiep-Trapegeer area (Fig. 8.1), an important shrimping ground close to the Belgian-French border, from May through December 1984. In April 1985 fish were obtained from the same area through the Fisheries Research Institute, Ostend.

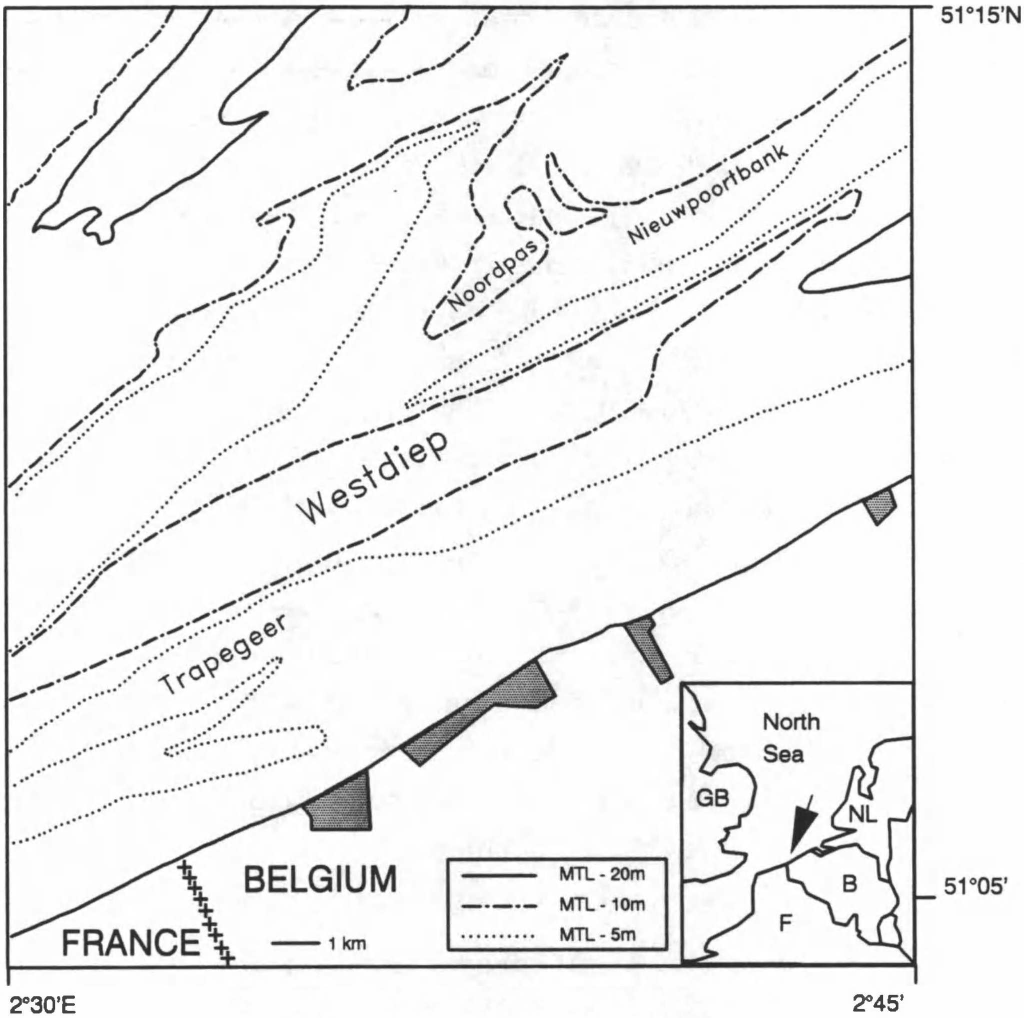


Fig. 8.1. Map of the study area in the Southern Bight of the North Sea (MTL is Mean Tidal Level).

In June and August 1985 two more samples were obtained from the O62. A composite picture of the seasonal patterns is obtained by combining the data from the two years. Mesh size was 20 mm stretched in the cod end. Most samples were collected during the night when goby catches were much higher than during the daytime (O. Hamerlynck unpubl. data). The April and May samples are daytime samples. In May catches were low and the fish from 4 hauls were pooled in order to have a large enough sample for stomach analysis. In September of 1984 two hauls from different depth strata were compared, one from the sandbank slope at about 8 m depth, the second one at about 18 m depth in the gully. The first haul was around sunset about 2 hours before low tide, the second haul was around 01 hours the next morning.

On board all fish were immediately anaesthetised in a Benzocaine (ethylamino-4-benzoate) solution in sea water, to avoid unnecessary suffering and to prevent regurgitation of the stomach content. Within 15 minutes after capture the fish were preserved in neutralised formaldehyde 7% final concentration. Shrinkage in formalin stabilises after a few hours and is less than 2 % (Healey 1971). In the laboratory, a few months after capture, standard length was measured and the fish were divided into 5 mm length classes. From the most abundant size classes occurring in both species, a maximum of 30 fish were selected at random for stomach analysis. In July no overlapping size classes of *P. minutus* (0+) and *P. lozanoi* (1+) could be found. As gobies do not have a functional sphincter between the stomach and the intestine, all food items in the entire gastro-intestinal tract, excluding the rectum, were identified, if possible, to species level. For calanoids, harpacticoids, and chaetognaths assigned ashfree dry weight (ADW) values, independent of the animals' length, were taken from the literature. For the radiole crowns of *Lanice conchilega* a visual volumetric estimate was compared to a volume of undigested radioles of known ADW. All other animals were measured, and their ADW prior to digestion was calculated from length-ADW regressions established for animals from the same area and from a similar shallow coastal area, the Voordelta (Appendix). The original size of incomplete prey was calculated from regressions relating unbroken parts, e.g. a telson or an antennal scale, to total length. All the stomach content data were analysed through the programme DRESAP (Cattrijsse 1987). Food composition is expressed as Gravimetric percentage (%G):

$$\%G = \frac{ADW\ prey\ type_i \times 100}{Total\ ADW\ of\ the\ ingested\ food}$$

which can be converted into energy units or to g carbon, and as Numerical percentage (%N):

$$\%N = \frac{Number\ of\ items\ of\ prey\ type_i \times 100}{Total\ number\ of\ prey\ items\ ingested}$$

Many indices have been proposed which combine %N and %G, and sometimes also percentage frequency (%F: the percentage of stomachs in which a certain item occurs) into a single index. The use of these composite measures should be discouraged as they tend to obscure rather than clarify food resource use (Berg 1979).

Data on the Fullness index (FI):

$$FI = \frac{DW\ of\ stomach\ contents\ x\ 100}{Total\ body\ ADW}$$

a measure of meal size or feeding intensity, are also presented.
As a simple measure of niche overlap, the shared utilisation of a resource by two species, the Renkonen index of similarity (Hurlbert 1978) was calculated from the numerical data of the different prey types for *P. minutus* and *P. lozanoi* from the same size range in the same haul:

$$C_{xy} = 1 - 1/2\ (\sum_i |p_{xi} - p_{yi}|)$$

where p_{xi} and p_{yi} are the proportions of prey species *i* in the total number of items in predator species *x* and *y*, respectively. To assess niche breadth the Shannon-Wiener diversity (Washington 1984) was calculated as:

$$H' = -\sum_i (p_i * \ln p_i)$$

There was a clear difference in the food intake between males and females in April and for the spawning period in April and May (Fonds 1973) results for the two sexes are presented separately. To demonstrate the link with spawning activity, data on the Gonado-somatic index (GSI):

$$GSI = \frac{Gonad\ ADW\ x\ 100}{Total\ body\ ADW}$$

where total body weight includes the gonad weight are presented, for both *P. minutus* and *P. lozanoi*. As FI and GSI are percentages the data were arc sin transformed for the calculation of mean and standard deviation and the results were then backtransformed (Sokal & Rohlf 1981). Differences in FI and GSI were assessed by non-parametric tests as the distribution of the transformed data was still significantly different from normal (Sokal & Rohlf 1981). Some males of both species, with aberrantly high testes weights, were excluded from the calculations.

Table 8.1. Size classes of fish and number of stomachs examined, number of prey items, Fullness Index (FI) and gravimetric and numerical food composition (main species) in *P. minutus* over the year.

Month	Jul	Aug	Sep_e	Sep_d	Oct	Dec	Apr ♂	Apr ♀	May ♂	May ♀
Fish size (mm)	30-40	40-50	30-65	35-65	35-50	40-50	45-50	45-50	45-60	45-60
Number of stomachs	84	86	191	163	90	60	13	9	15	34
Number of items	609	707	9744	990	1463	568	827	373	252	601
FI	0.16	0.19	0.39	0.12	0.34	0.20	0.59	0.09	0.17	0.39
Prey species	Gravimetric percentage (%G)									
Bivalvia species	4	31	87	16		86	30	53	4	
Stenelais boa					5				6	
Nephtys hombergi										
Capitella capitata									23	
Lanice conchilega	14	17			16				4	19
Pectinaria koreni				53			12			
Temora longicornis					5			41	9	8
Pariambus typicus	30	10			4					
Atylus swammerdami									4	
Bathyporeia species									7	
Gammarus crinicornis									22	30
Maera grossimana									6	
Gastrosaccus spinifer							14			
Schistomysis spiritus	30		5		59	8				
Crangon crangon	12	23		13						
Pontophilus trispinosus										15
Pomatoschistus eggs							41		6	
Pomatoschistus species		12								
Prey species	Numerical percentage (%N)									
Bivalvia species			7			19				
Lanice conchilega	9	10			4	5				
Tisbe furcata	4									
Temora longicornis			40	26	52	6	7	94	63	80
Pariambus typicus	56	49	17	28	17	44				
Gammarus crinicornis										9
Microprotopus maculatus	9	20	28	18	14	18				
Pseudocuma longicornis		5								
Schistomysis spiritus					8					
Crangon crangon		4								
Pomatoschistus eggs							91		26	

RESULTS

A total of 9398 fish were examined and the contents of 745 stomachs were analysed (Table 8.1). Results are presented in a sequence from the first capture of 0+ juveniles in July to the last 1+ adults caught in May. In June only 7 adult *P. minutus* were caught, an insufficient number for stomach analysis.

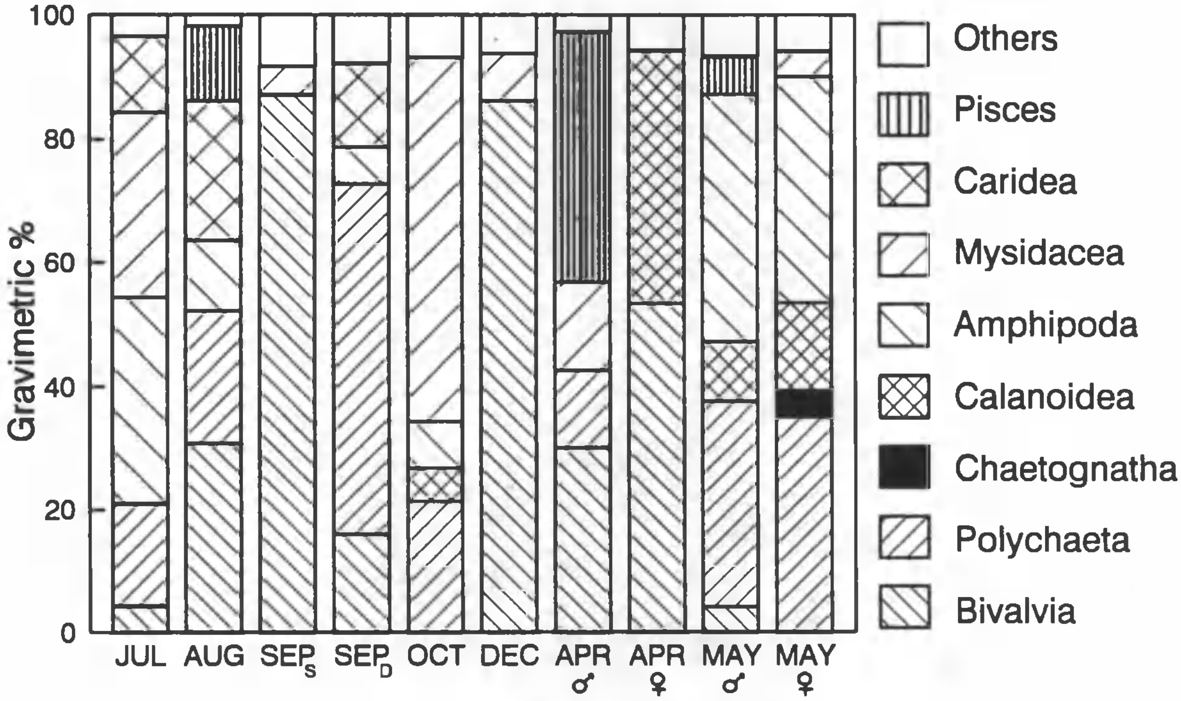


Fig. 8.2. Gravimetric food composition (%G as ADW) for *Pomatoschistus minutus* over the year.

Gravimetric food composition is given in Table 8.1 (main species: representing more than 4 %) and summarised (main taxonomic groups) in Fig. 8.2. In July the 0+ juveniles fed mainly on the caprellid amphipod *Pariambus typicus* and on the mysid *Schistomysis spiritus*. Radiole crowns of the sedentary polychaete *Lanice conchilega* and small juveniles of the shrimp *Crangon crangon* were of subsidiary importance. In August these last two species became more important but bivalve siphons were dominant. In September a large difference in feeding activity was noted with about 8 times as many food items per stomach in the shallow station in comparison with the deep station. There was a significant difference in FI (Table 8.1) between the two hauls (Mann-Whitney U = 5672; $p << 0.001$). Bivalve siphons were by far the most important prey item in the shallow station. In the deeper station the sedentary polychaete *Pectinaria koreni* was the dominant item, with some bivalve siphons and shrimp. In October *Schistomysis spiritus* was again the dominant food, with *Lanice* also relatively important. In December it were bivalve siphons again plus some *Schistomysis*. In April there was a very pronounced difference between the food of the males and the females. Males depended mainly on eggs of *Pomatoschistus*, bivalve siphons, *Pectinaria* and the benthic mysid *Gastrosaccus spinifer*. Females fed mainly on bivalve siphons and the pelagic copepod *Temora longicornis*. Though FI in the males seems higher than in the females (Table 8.1) this difference was not significant due to small sample size and large individual variability. In May there was much less difference between males and females. Both sexes fed mainly on polychaetes and gammaridean amphipods. The sedentary polychaete *Capitella capitata* was dominant in the males. In the females the gravimetric picture was a bit biassed because of the importance of a single large *Nephtys*. *Gammarus crinicornis* was important for both sexes.

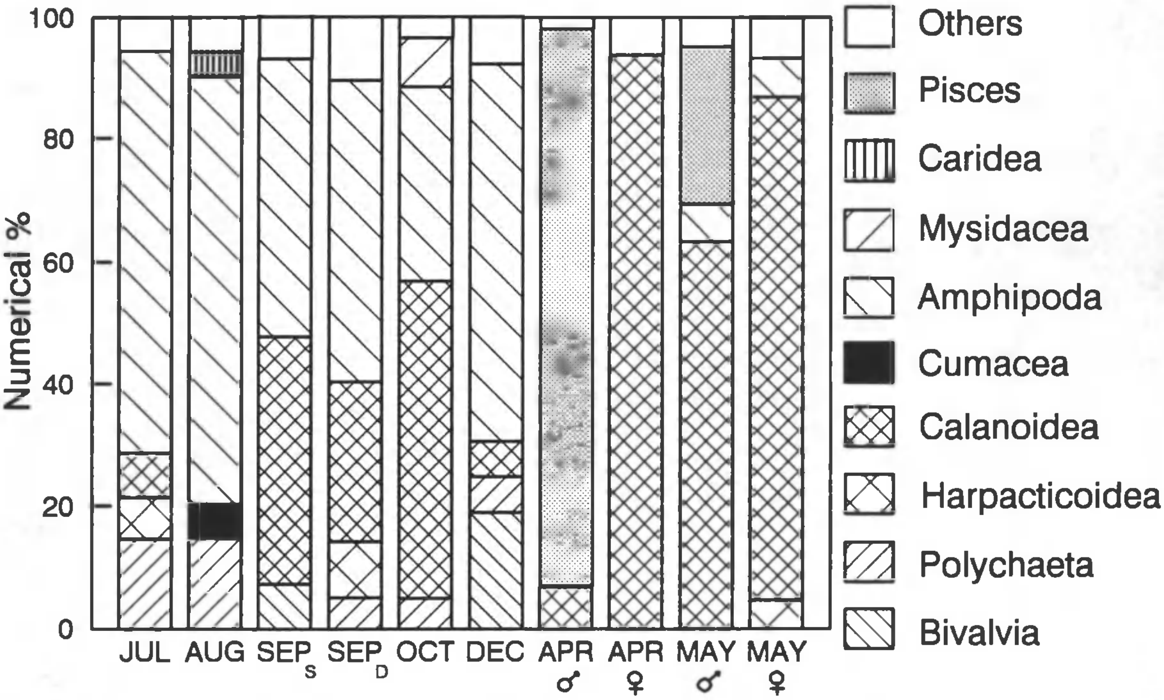


Fig. 8.3. Numerical food composition (%N) for *Pomatoschistus minutus* over the year.

Numerically the picture is rather different (Table 8.1, Fig. 8.3) with *Pariambus typicus* and the small gammaridean amphipod *Microprotopus maculatus* as prominent items throughout summer and autumn. In September and October *Temora longicornis* was also important. It became the dominant item in spring. In the males the eggs of *Pomatoschistus* were the dominant item in April and were still quite important in May.

The change in food composition with size, recorded at the shallow station in September, is shown in Fig. 8.4. Gravimetrically (Fig. 8.4a) bivalve siphons dominated except in the smallest size class (30-35 mm). Mysids gradually decreased in importance with increasing fish size. All other groups were relatively unimportant in weight terms. Numerically bivalve siphons were only important in the largest size classes (Fig. 8.4b). Both calanoid and harpacticoid copepods were taken in decreasing proportion by larger fish. They were gradually replaced by large numbers of *Microprotopus maculatus*. *Pariambus typicus* was taken at a more or less constant level by all size classes.

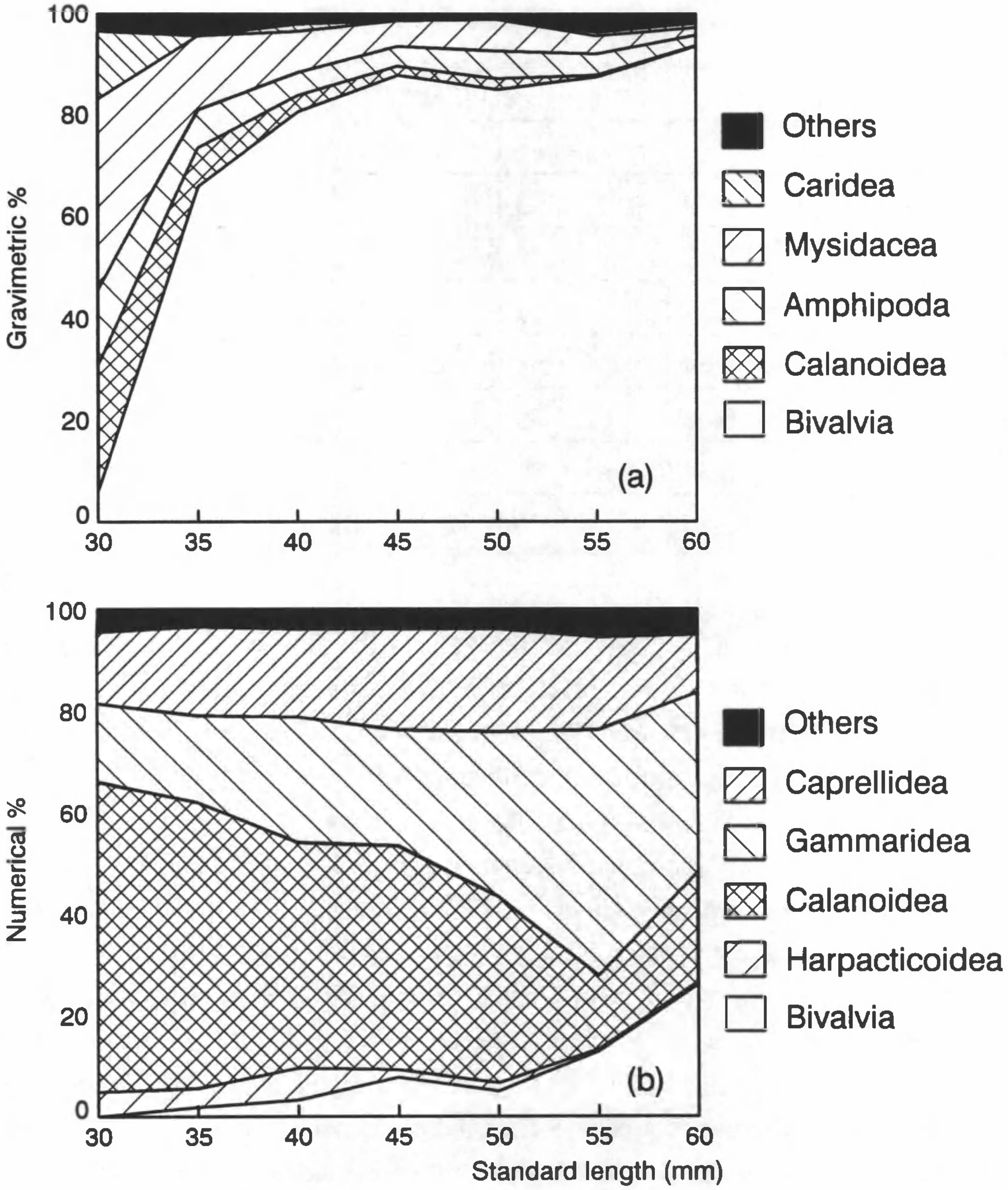


Fig. 8.4. Food composition of different size classes of *Pomatoschistus minutus* in September: (a) gravimetrically (%G), (b) numerically (%N).

Niche overlap and diversity are shown in Table 8.2. Niche overlap was highest in May and in August 1984 and lowest in April and December. Shannon-Wiener diversity was usually about twice as high in *P. minutus* than in *P. lozanoi*, except in the August samples of both years and in December.

Table 8.2. Niche overlap between *P. minutus* and *P. lozanoi* as measured by the Renkonen index and niche breadth as measured by the Shannon-Wiener index for the different months.

Month	Renkonen	Shannon-Wiener	
		P. minutus	*P. lozanoi*
August 1984	0.79	1.13	1.15
August 1985	0.55	2.32	2.15
September	0.57	1.53	0.65
October	0.64	1.58	0.84
December	0.46	1.69	1.91
April	0.34	0.85	0.12
May	0.85	0.90	0.40

The evolution of the GSI over the year in the females of *P. minutus* (Fig. 8.5a) shows a maximum of about 25 % of total body weight in April. In May there is a significant decrease in mean GSI (Mann-Whitney $U = 55$, $p = 0.005$). In the 0+ group between July and December there is only a very minor increase in the GSI noticeable. In April and May the GSI in *P. lozanoi* is rather similar to the GSI in *P. minutus*. During the presumed spawning season between June and August GSI is significantly lower (Mann-Whitney $U = 626$, $p << 0.001$) than in April-May. In the male *P. minutus* the time trajectory of the GSI is similar to that in the females except that the values are of course much lower. The GSI in male *P. lozanoi* is about half as high as in *P. minutus*. This difference is highly significant (Mann-Whitney $U = 181$, $p << 0.001$). During the spawning season male *P. lozanoi* with aberrantly high testes weights could be diagnosed as being 'sneaker' males because externally they looked like females, including the distended silvery abdomen and the typical chin pigmentation (Hamerlynck 1990), and that the sperm duct gland was undeveloped. Large testes were also noted in a number of individuals of both species outside of the spawning season (Table 8.3). Size, scale readings (Moreira *et al.* 1991) and gonad structure suggested these were 0+ fishes and not post-spawners.

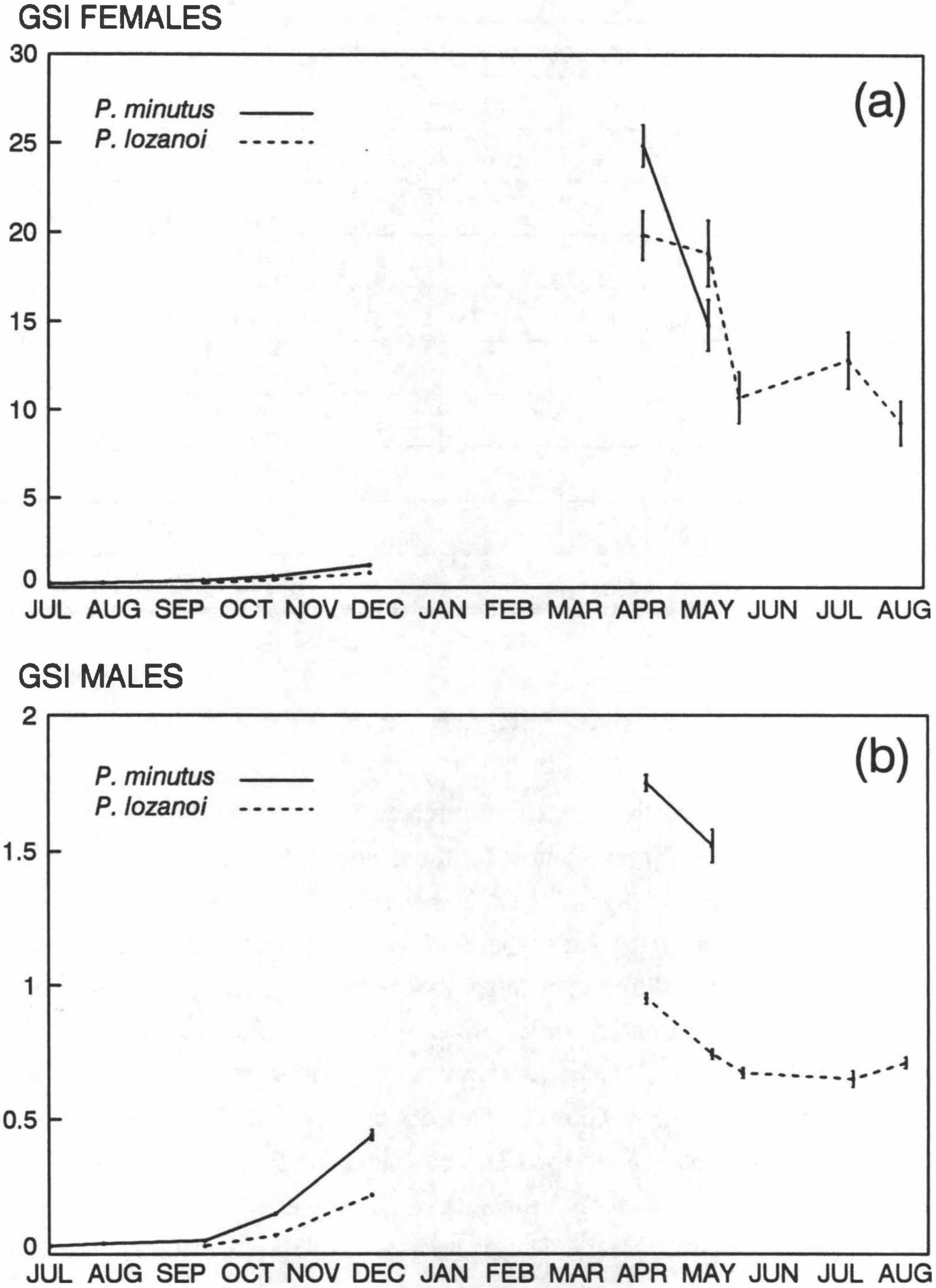


Fig. 8.5. Pattern in average GSI (with standard deviation) for *Pomatoschistus minutus* and *Pomatoschistus lozanoi* over the year: (a) females, (b) males.

Table 8.3. Average Gonado-somatic index (GSI, backtransformed arcsin transformed) and number of testes examined for normal and sneaker male gobies in the different months.

Month	*P. minutus*				*P. lozanoi*			
	normal ♂		sneaker ♂		normal ♂		sneaker ♂	
	GSI	N	GSI	N	GSI	N	GSI	N
July	0.03	49			0.65	33	3.15	2
August	0.04	37			0.71	20	2.15	1
September	0.05	114	0.73	3	0.03	64	0.22	2
October	0.15	25	1.43	2	0.07	48	0.31	1
December	0.44	19			0.22	23		
April	1.75	13			0.95	21	5.31	1
May	1.52	14			0.74	38		
June					0.67	42		

DISCUSSION

As recorded in other areas (see references in the introduction) *P. minutus* fed on a wide variety of prey items. In the study area these were mainly pelagic copepods, hyperbenthic mysids, small epibenthic crustaceans, benthic polychaetes and bivalve siphons. *P. minutus* therefore is a versatile small carnivore with the capacity to use very different feeding modes such as biting and suction feeding, which suggests its morphodynamics are unspecialised (Barel 1983, Aerts 1992). In September the food of *P. minutus* shows a remarkable resemblance to the food of young flatfishes (Ansell & Gibson 1990), an indication of its preference for benthic food rather than hyperbenthic food as was found for *P. lozanoi* (Hamerlynck *et al.* 1990). As *P. minutus* and *P. lozanoi* have quite a different food niche, except in low-diversity estuarine areas (Claridge *et al.* 1985), the studies which did not distinguish between the two species may be difficult to interpret.

As can be seen from the large difference in %G and %N composition (Table 8.1, Figs. 8.2 & 8.3), *P. minutus* consumed a wide size range of prey and especially large numbers of very small prey which contributed little to the %G. Similarly

Zander (1990) found no correlation between *P. minutus* size and prey size and Magnhagen (1985) found that *P. minutus* took a higher proportion of small *Corophium* than their occurrence in the environment. Possibly, when increasing in size, the fish become progressively capable of taking larger items and a wider range of species, but still fall back on skills acquired as small juveniles in feeding on *Temora longicornis*, *Microprotopus maculatus* and *Pariambus typicus*, which were energetically more rewarding early in life. Bivalve siphons, possibly from *Spisula subtruncata*, the dominant bivalve in the area, were of particular importance in the %G composition. Like the cropping of the radioles of *Lanice conchilega* this is a special type of predation which probably does not cause significant mortality in the prey. The extra production by regenerating parts of the benthos is not usually taken account of in studies of secondary production (Vlas 1985). When such predation is important, special care should be taken when proposing food-limitation hypotheses on the basis of a comparison of benthic production (often simply based on P/B ratios) and epibenthic consumption.

In September in the deeper station the sedentary polychaete *Pectinaria koreni* was the dominant item. At that time of night about a dozen shrimping vessels was continuously covering the same ground and possibly the *Pectinaria* were removed from the sediment by the ploughing activity of the tickler chains. It seems unlikely that *P. minutus* can retrieve buried *Pectinaria* from the sand. The low feeding activity at the deep station in comparison to the shallow station may be related to circadian or circatidal feeding rhythms not uncommon in Gobiidae (Gibson 1993, Hamerlynck *et al.* submitted a).

The importance of caprellid amphipods in *P. minutus*, not normally an important component of fish diets (Caine 1991), is remarkable.

It was originally thought that part of the success of small Gobiidae was due to their ability to exploit the meiofauna (Miller 1979). However, meiofauna were generally unimportant in the size classes investigated in the present study and Gee (1987) also reports only a small impact of gobies on meiofauna. In some special environments such as the Baltic (Aarnio & Bonsdorff 1993) and the Oosterschelde (Hamerlynck & Vanreusel in press) meiofauna are of greater importance for Gobiidae. However, it should be taken into account that Aarnio & Bonsdorff (1993) reported only the numerical percentage of the prey items and, as can be seen from Table 8.1, high numerical percentages of small animals, such as copepods, do not necessarily feature prominently in the gravimetric food composition. Smaller *P. minutus* size classes than investigated in the present study are unlikely to be more dependent on benthic harpacticoid copepods as they are more pelagic and feed on zooplankton (Evans 1983, Thorman & Wiederholm 1986, Mehner 1992).

The Renkonen index represents a geometric area of intersection of the probability density functions of both species with respect to a given resource axis (Hurlbert 1978). It is certainly not a measure of competition. A high overlap index is neither a necessary nor a sufficient condition for competition (Colwell & Futuyma 1971). Still, it is the only index that can be used here as it does not require any information on the resource state abundance (Hurlbert 1978). When comparing food consumption by *P. minutus* with consumption by *P. lozanoi* from the same size classes in the same haul (Hamerlynck *et al.* 1990), the highest overlap (Table 8.2) was noted in May when both species relied extensively on *Temora longicornis*. In August of 1984 overlap was also quite high, with both species taking *Lanice* and *Pariambus*. In August 1985 overlap was much lower. Though both species took largely the same species they did so in different proportions, with *P. lozanoi* taking more *Pseudocuma longicornis* and *Lanice* and *P. minutus* taking more *Microprotopus maculatus*. In October the high overlap was mainly due to the shared use of again *Temora* and of *Schistomysis spiritus*. Overlap was especially low in April, when *P. minutus* males had a highly aberrant food consumption with a predominance of *Pomatoschistus* eggs. The conclusion is that there was always a shared use of resources and that, at times, the overlap was quite considerable. In relation to the potential for competition between the two species the high overlap in May is unlikely to be an indication of competition as it coincides with the huge spring bloom of *Temora* in the area (Daro & Gijsegem 1984) and as population size of both gobies is at its lowest in late spring (Fonds 1973). In autumn a second bloom of *Temora* can occur, lasting until December (M.H. Daro pers. comm.). Similarly, the large overlap in the use of *Schistomysis spiritus* coincided with the autumn peak in its abundance in the Voordelta (Mees *et al.* in press a), so again this species may not have been a limiting resource. In general, small Gobiidae of open ground are thought to be predator- rather than food-limited (Miller 1979, Evans 1983, Thorman & Wiederholm 1986). Still, Pihl (1985) suggested gobies were competing with other epibenthic predators for a limited benthic food supply in a habitat adjacent to the site of Evans (1983). However, the main difference between the results of the two studies was related to the use of different conversion factors (Gee 1989). Sand gobies seem not to be able to affect their prey populations in intertidal mud flats (Gee 1987, Jaquet & Rafaelli 1989), though statements of the contrary can also be found (Schmidt-Moser & Westphal 1981). Aarnio *et al.* (1991) also did not report any effect of *P. minutus* on the colonisation of defaunated sediment by benthic animals.

With regard to niche breadth (Table 8.2) *P. minutus* can be considered a generalist in comparison to the more specialised *P. lozanoi*. Only in August and December was the niche breadth of *P. lozanoi* in the same range as that of *P. minutus*. The niche expansion of *P. lozanoi* in August is linked to a niche shift from hyperbenthic to benthic feeding (Hamerlynck *et al.* 1990) and its interpretation is difficult. Changes in many factors coincide in August and the elucidation of their relative contributions would require experimental studies, data on goby abundance and daily ration, and an assessment of the complete resource base. First, August was the time of the, as yet unexplained, near total absence of Mysidacea from a comparable shallow coastal area (Mees *et al.* in press a). Next, in August the adult *P. lozanoi* were still spawning (Fonds 1973, this study) and may therefore have been confined to benthic feeding in close proximity to the nesting sites. Likewise, in April, when *P. minutus* was spawning, the adult males fed nearly exclusively on benthic animals at a time when similar sized *P. lozanoi* fed on pelagic *Temora* and small 0+ *P. minutus* (Hamerlynck *et al.* 1990). Thirdly, in August the major part of the *P. minutus* population belonged to size classes below the mesh selection size. These small sand gobies feed on small items, possibly mainly pelagic copepods. The release from interference competition by large *P. minutus* may have allowed *P. lozanoi* to expand its realised niche to its fundamental niche (Hutchinson 1958) which may be benthic feeding. Conversely, the high densities of pelagic feeding small *P. minutus* may have forced *P. lozanoi* to assume a more benthos-oriented feeding strategy. In December the high diversity in the food of *P. lozanoi* was linked to a low overlap, so both species ate a different but diverse diet. In *P. lozanoi* the high diversity was mainly due to a number of prey species which occurred only as single items. In conclusion, the evidence for interference competition between the two species from the crude field data in the present study, is equivocal. A comparison of the morphodynamics (Aerts 1992) of feeding in both species would be of major interest.

The GSI data correspond well to the spawning periods proposed for both species by Fonds (1973). Unfortunately no samples could be obtained between mid December and mid April, the time when the increase in GSI occurred. Judging from the graphs in Rogers (1988a) GSI in female *P. microps* increased quite dramatically about two months before the start of spawning in early May and decreased when spawning started. Female GSI in the present study was higher than the data for *P. minutus* given in Healey (1971), who found a maximum of about 12 %, and lower than those reported for *P. microps* by Rogers (1988a). Healey's (1971) data concern wet weight GSI and refer to gobies that remained in the estuary, while the spawners emigrated to the sea. Rogers (1988a) reported Dry weight GSI expressed as a percentage of lean body weight, excluding the gonads. In the present study maximal lean body weight GSI for female *P. minutus* and *P. lozanoi* was recorded in April at 35.4 and 27.2 respectively, which is probably still lower than the results of Rogers (1988a). The smaller *P. microps* may therefore channel more energy into reproduction than *P. minutus* and *P. lozanoi*. The data in Claridge *et al.* (1985) concern wet weight GSI expressed as a percentage of total body weight for fish stored in alcohol. A comparison with these data is therefore difficult. They recorded a steep increase in GSI in female *P. minutus* in late February. However, the data are less reliable as they caught only a few fish on migration from the estuary to the spawning grounds. Apparently Claridge *et al.* (1985) found lower GSI in female *P. lozanoi* than in *P. minutus*. In the males some data points were also suggestive of a lower GSI in male *P. lozanoi* but fluctuations in the means were rather large and no error bars were provided.

The importance of *Pomatoschistus* eggs in the stomachs of male *P. minutus* in spring lends support to the hypothesis that nest sites may be a limiting resource (Nellbring 1986), and that male sand gobies compete strongly for them (Lindström 1988, Magnhagen & Kvarnemo 1989). Surprisingly, no *Pomatoschistus* eggs were found in the high numbers of spawning male *P. lozanoi* examined, suggesting that intraspecific competition for shells, or at least aggressive take-over of occupied spawning sites, is less important in this species. Perhaps population size at the time of spawning is so low that, for *P. lozanoi*, shells are not a limiting resource. On the other hand interspecific competition for nest sites is a distinct possibility: judging from the GSI in female *P. lozanoi* the animals are ready to spawn in April but apparently only start in June. In aquaria *P. lozanoi* started spawning in early to mid April over a range of temperatures from 10-15 °C (Fonds 1973). The temporal segregation of spawning may be therefore be an outcome of interference competition by the larger *P. minutus*, which may exclude the smaller *P. lozanoi* males from establishing territories.

The existence of alternative reproductive tactics, already observed in a number of Gobiidae (Cole 1982, review in Miller 1984), is confirmed for both *P. minutus* and *P. lozanoi*. The higher GSI in sneakers is evident from Table 8.3, though sample sizes were too small for reliable statistical testing. Assuming that the large testes found outside the breeding season represented the early development of sneaker testes, sneaker males would represent about 2 % of males in both species.

This goes counter the contention, based on the stomach content data, that competition for nest sites may be less strong in *P. lozanoi*. The existence of a clear anatomical difference between the two types of male and the hypothesis that sneaker male testes may start growing long before the start of the spawning season, suggest there may be a genetic basis for the alternative strategy, which may exist as an evolutionary stable strategy or ESS (Vincent & Brown 1988). Magnhagen (1992) found sneaking to be an opportunistic strategy of small anatomically 'normal' males in *P. microps*, but this just indicates that there is scope for a selective advantage of the sneaker strategy. Unfortunately, as in the present study fishes were selected on the basis of size range overlap between the two species, it is not possible to compare the size-frequency distribution of sneaker and normal males to assess if large testes were more common in smaller males as found by Cole (1982). There is certainly much scope for further investigations into *Pomatoschistus* tokology, both in energetics as set out by Rogers (1988a and b) examining both males and females in more species and along latitudinal gradients, and in ethology as set out by Magnhagen & Kvarnemo (1989) and Magnhagen (1992).

ACKNOWLEDGEMENTS

Luk Bogaert, the skipper of the shrimping vessel O62 'Seabird II', kindly allowed us to stand in the way and pick out the gobies before they were cooked. The hospitality of skipper and crew was greatly appreciated. Colin Janssen's voluntary help with the field work is also acknowledged. Dr. F. Redant of the FRI, Ostend kindly provided some of the samples. The second author acknowledges a grant from the Institute for the Encouragement of Scientific Research in Industry and Agriculture (IWONL). The project was also supported by the Concerted Actions Oceanography of the Ministry of Scientific Policy and by the Belgian FKFO project 32.0086.88.

Chapter 9

Differences in food resource use and competition in two species of Gobiidae *Pomatoschistus minutus* and *Pomatoschistus lozanoi* in a shallow coastal area

ABSTRACT

Data are presented on the food of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* collected in autumn along a gradient in the shallow coastal area in front of the Dutch Delta. The gradient went from a sheltered lagoonal area with low tidal current velocity to a wave-exposed area with high tidal current velocity. This gradient coincides with a decreasing gradient in macrobenthic, hyperbenthic, epibenthic and fish biomass. Food resource overlap at the different localities was compared with relative prey abundance, i.e. food present per g goby. The hypothesis H_1 being tested was that food competition was the mechanism which caused the differences in food resource use observed in *P. minutus* and *P. lozanoi*. No decreasing trend in resource overlap could be detected when moving from localities with a high relative food abundance to areas with a low relative food abundance. A very low overlap was only detected in gravimetric terms in the locality with the lowest relative food abundance. As fish were not feeding very actively at this locality, this result may have been biassed by a single large food item. Therefore, interspecific competition for food was unlikely to have been the mechanism causing the observed differences in resource use in the size class of gobies investigated.

INTRODUCTION

In a study in the Belgian coastal waters Hamerlynck *et al.* (1990) and Hamerlynck & Cattrijsse (submitted) found fairly straightforward differences in food resource use between the morphologically similar congeners *Pomatoschistus minutus* and *Pomatoschistus lozanoi*. The first species preferred benthic and epibentic prey and the second species preferred hyperbenthic and pelagic prey throughout most of the year. On the basis of calculations of niche breadth they concluded that *P. lozanoi* was a more specialist species in comparison to *P. minutus*. In August however, a strong niche shift towards benthic feeding was recorded in *P. lozanoi*, which was correlated with a niche expansion. In the absence of data on the abundance of the predators and their prey, it was impossible to evaluate these niche changes in relation to potential interspecific competition. Hamerlynck & Cattrijsse (submitted) obtained their fish from a shrimp trawler. Each haul, took between 30 minutes and 2 hours depending on shrimp abundance and therefore covered a lot of ground. Habitat partitioning, which may have been the underlying cause of the difference in food resource use, was possibly obscured.

Besides predation, mutualism, parasitism and disease, competition is potentially one of the major structuring forces in ecological communities (e.g. Niemelã 1993). Interesting recent critical reviews on competition as a force in ecology and evolution are Arthur (1987), Keddy (1989) and Peters (1991).

In the present study relative food abundance (per g of predator) and food resource use by two species of goby were compared at different sites along an environmental gradient. The hypothesis H_1 is that food competition is the mechanism which caused the differences in food resource use observed in *P. minutus* and *P. lozanoi*.

MATERIALS AND METHODS

The Voordelta is the shallow coastal area formed by the interlinked ebb tidal deltas of the (former) estuaries of the rivers Schelde, Meuse and Rhine. The study area proper covers the central part of the Voordelta (Fig. 9.1), including the ebb tidal deltas of the former Grevelingen estuary and of the Oosterschelde. As a result of large-scale coastal engineering, major changes have occurred in the geomorphology (Louters *et al.* 1991) and ecology (Hamerlynck *et al.* 1992) of the Voordelta. In summary, as a consequence of the reduction in current velocities and wave action, the ebb tidal delta of the Grevelingen has become a lagoonal system, comparatively rich in hyperbenthos (Mees & Hamerlynck 1992), macrobenthos (Hamerlynck *et al.* 1992), epibenthic invertebrates and fishes (Hamerlynck *et al.* in press). In the gullies, the ebb tidal delta of the Oosterschelde has some areas rich in benthic life but in general the area is poorer than the ebb tidal delta of the Grevelingen (Hamerlynck *et al.* 1992, Hamerlynck *et al.* in press). The more offshore, wave exposed sandy area of the Banjaard is very poor in macrobenthos, fishes and epibenthic invertebrates (Hamerlynck *et al.* in press). As a consequence, important gradients in prey abundance exist in the area at a scale which can be sampled quasi-synoptically.

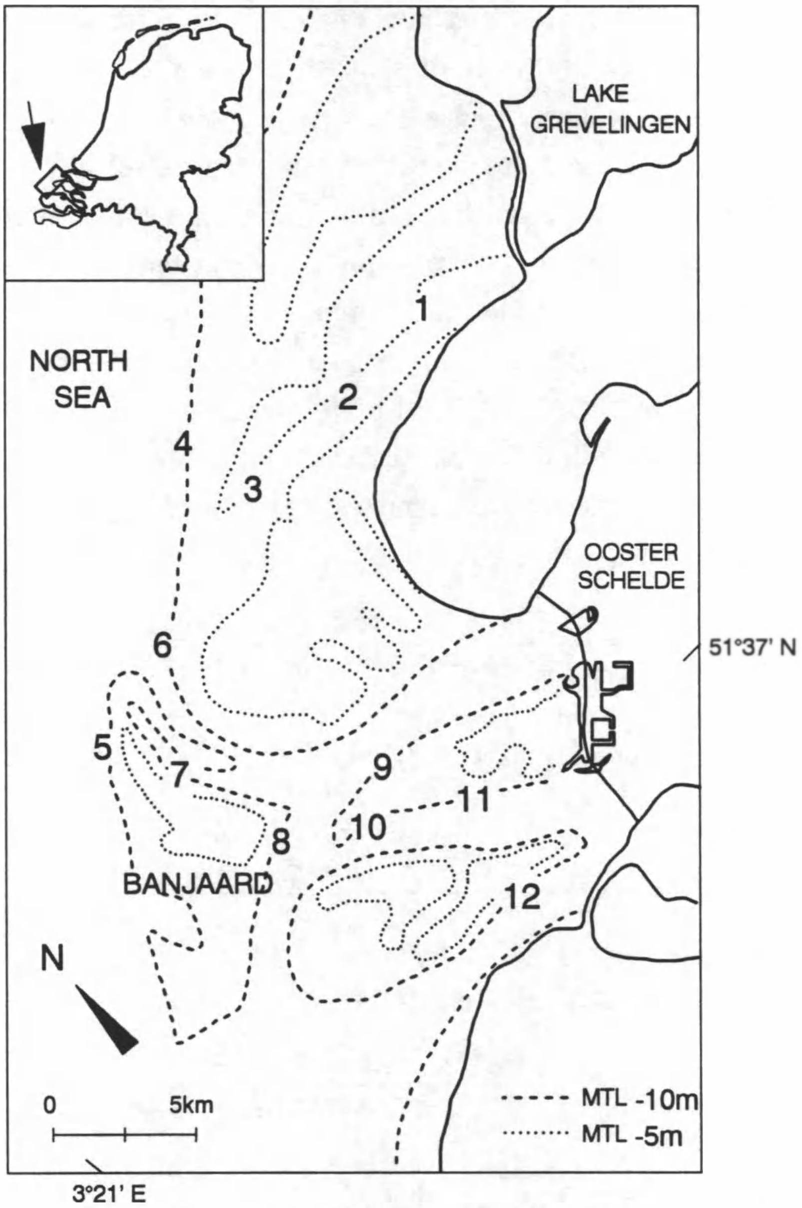


Fig. 9.1. Map of the study area with the 12 sampling localities. MTL stands for Mean Tidal Level.

On 3, 4 and 5 November 1987 samples were taken at 12 localities in the area (Fig. 9.1). At each locality 3 hauls were made following the 5, 8 and 10 m below Mean Tidal Level (MTL) depth contour. Each haul was 1000 m long (radar readings from fixed points). Gobies were caught using a three meter beam trawl operated from the port side of the vessel and concomitantly the hyperbenthos was sampled using a sledge (Hamerlynck & Mees 1991) operated from starboard. On board all fish were immediately anaesthetised in a Benzocaine (ethylamino-4-benzoate) solution in sea water, to avoid unnecessary suffering and to prevent regurgitation of the stomach content. Within 15 minutes after capture fish and hyperbenthos were preserved in neutralised formaldehyde 7% final concentration. In the laboratory all fish were identified, measured (standard length) and split into 5 mm size classes.

For the comparative study of stomach contents, the localities 1, 2, 4 and 5 were selected on a gradient from a sheltered lagoonal area with low tidal current velocity to a wave-exposed area with high tidal current velocity. Locality 10 in the ebb tidal delta of the Oosterschelde was also selected because it is a sheltered area with high tidal current velocity. From single hauls at these localities a maximum of 20 fish of each species of the 45-50 mm size class were selected for stomach analysis (Table 9.1). To check if important size related changes in food resource use occurred, fishes from the 40-45 (20 of each species) and 50-55 mm size classes (20 *P. minutus* and 18 *P. lozanoi*) from the haul at locality 4 were also analysed. The methodology used for the stomach analyses is described in Hamerlynck & Cattrijsse (submitted). Food composition is expressed as Gravimetric percentage (%G):

$$\%G = \frac{ADW\ prey\ type_i\ x\ 100}{Total\ ADW\ of\ the\ ingested\ food}$$

which can be converted into energy units or to g carbon, and as Numerical percentage (%N):

$$\%N = \frac{Number\ of\ items\ of\ prey\ type_i\ x\ 100}{Total\ number\ of\ prey\ items\ ingested}$$

Data on the Fullness index (FI, Berg 1979):

$$FI = \frac{DW\ of\ stomach\ contents\ x\ 100}{Total\ body\ ADW}$$

a measure of meal size and feeding intensity, are also presented.

As a simple measure of niche overlap, the shared utilisation of a resource by two species, the Renkonen (1938) index of similarity (Hurlbert 1978) was calculated from the gravimetric data of the different prey species for *P. minutus* and *P. lozanoi* from the same size range in the same haul:

$$C_{xy} = 1 - 1/2 \left(\sum_{i} |p_{xi} - p_{yi}|\right)$$

where p_{xi} and p_{yi} are the proportions of prey species i in the total weight of items in predator species x and y, respectively. The analogous calculations were also done using the numerical data.

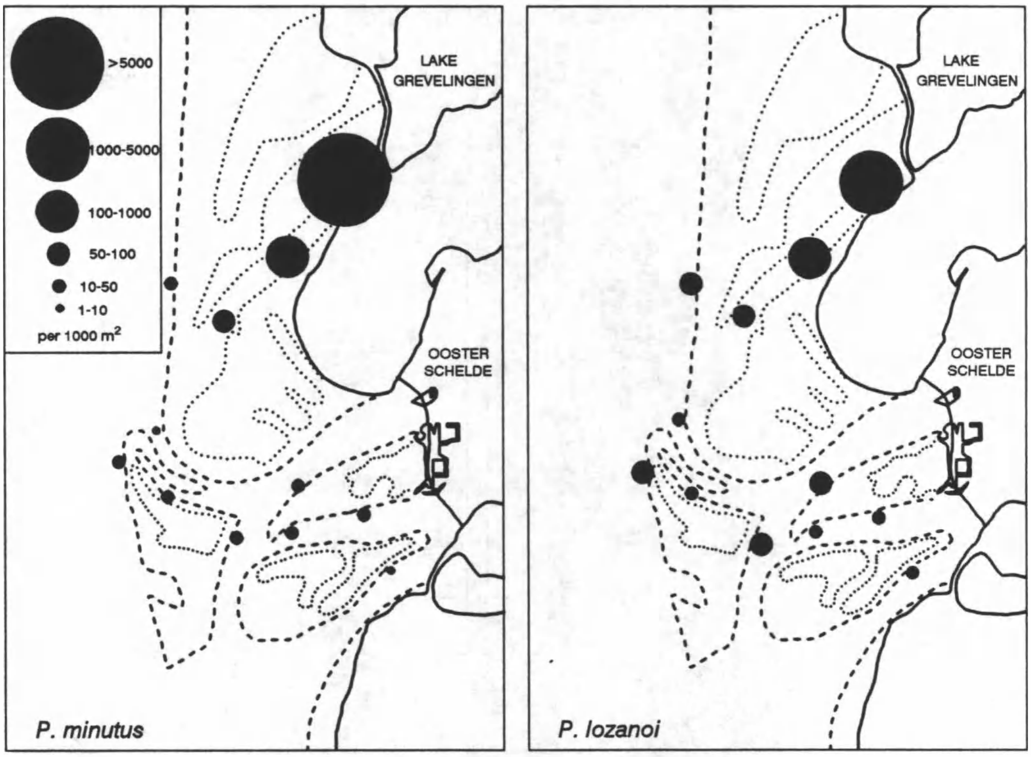


Fig. 9.2. Average abundance (numbers per 1000 m²) of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* at the 12 localities (means of three hauls).

All animals in the hyperbenthic samples were identified and counted. From the dominant species at least 60 individuals were selected at random for measurement. Using length-Ashfree Dry Weight (ADW) regressions, hyperbenthic biomass was calculated for the hauls selected for stomach analysis.

The macrobenthos data were collected in the autumn of 1988 according to the methodology described in Hamerlynck *et al.* (1992). Although in the Voordelta the abundance of individual macrobenthic species may vary strongly among years (1986-1989), total density, biomass, community structure and spatial extent of the communities were quite constant (Craeymeersch *et al.* 1990, J.A. Craeymeersch unpubl. data).

Net efficiency for gobies and hyperbenthic animals was assumed to be 100 %. Creutzberg *et al.* (1987) found that, on sandy bottoms, catches of *Pomatoschistus* species increased significantly as a function of the number of tickler chains used. Net efficiency of bottom gear is usually estimated to be between 10 and 50 % (e.g. Kuipers 1975; Mearns & Allen 1978; Evans & Tallmark 1979; Elliott & Taylor 1989). Therefore goby density and biomass figures probably have to be at least doubled. No data exist on the efficiency of benthic sledges, but it is well known that Mysidacea, the main component of the hyperbenthos, are very apt at net avoidance (Mauchline 1980).

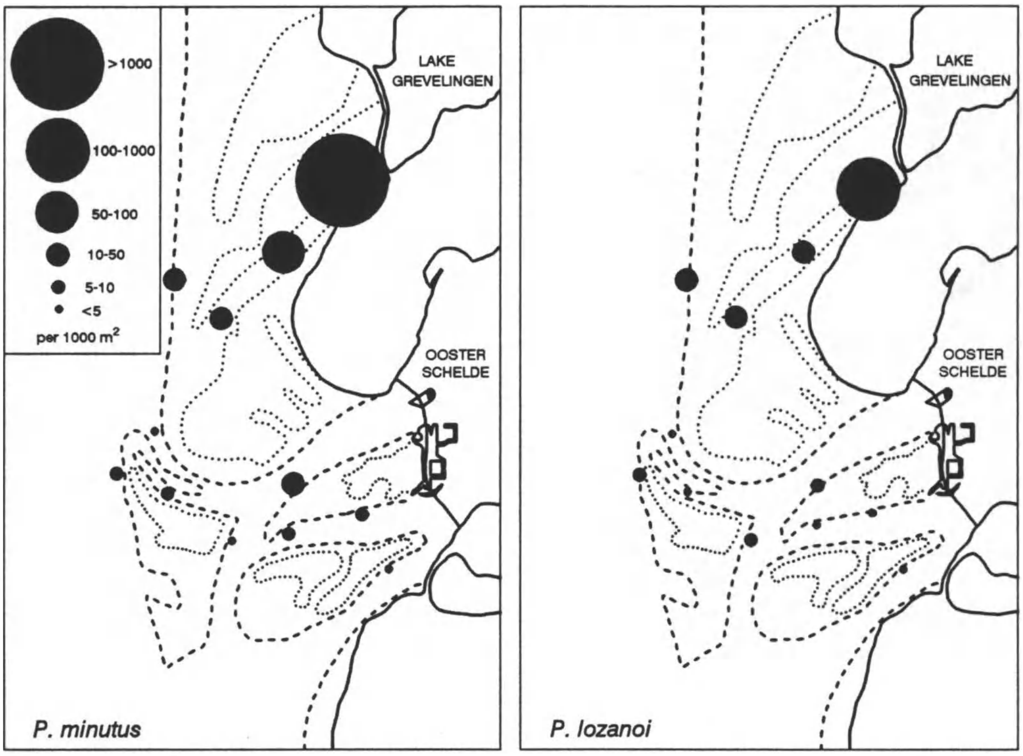


Fig. 9.3. Average biomass (g ADW per 1000 m^2) of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* at the 12 localities (means of three hauls).

Backtransformed arcsin transformed Fullness Indices were tested for significant differences by the Mann-Whitney U test (Sokal & Rohlf 1981) in pairwise comparisons between localities and between species at each locality. The relevant significance level was calculated as 0.05 divided by the number of comparisons according to the Bonferroni principle (Fry 1993).

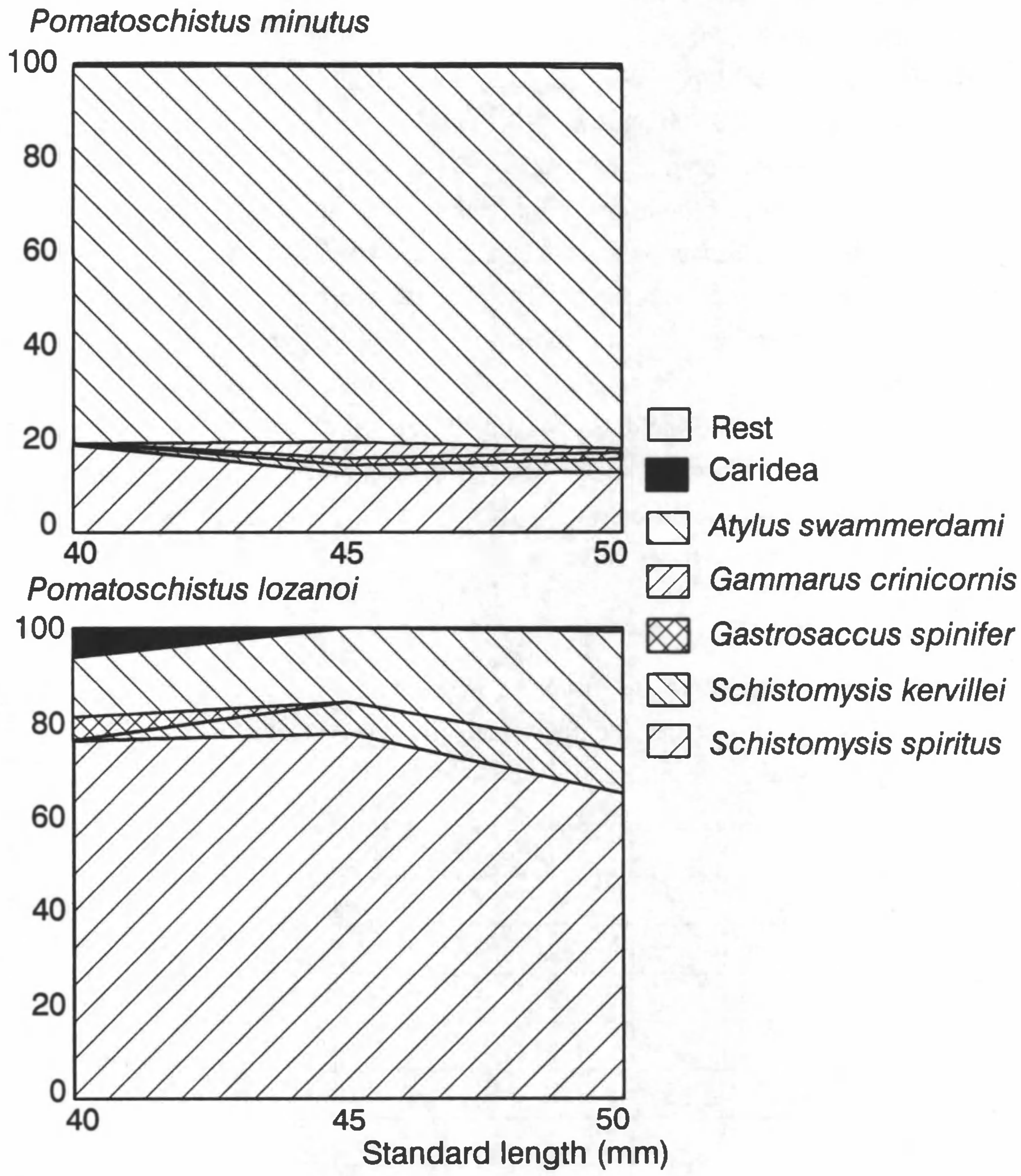


Fig. 9.4. Food composition (%G as ADW) for three size classes of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* at locality 4.

RESULTS

Average density and biomass per locality of the two goby species are shown in Figs. 9.2 and 9.3. The distribution of both species was uneven, with densities in the ebb tidal delta of the former Grevelingen estuary increasing from the sea towards the dam (Fig. 9.2). At the 10 m depth station, closest to the dam, density of *P. minutus* even exceeded 10 gobies per m² (equivalent to a biomass of 6.4 g ADW per m²). Outside of this area densities in general did not exceed 30 *P. minutus* per 1000 m². The prime habitat for *P. lozanoi* was also the ebb tidal delta of the Grevelingen (highest density over 3 per m², equivalent to a biomass of 0.4 g ADW per m²). Densities of about 60 *P. lozanoi* per 1000 m² were recorded at a few sites in the Banjaard area and the ebb tidal delta of the Oosterschelde. In terms of biomass (Fig. 9.3) the distribution of both species resembles the density distribution. Even in localities where *P. lozanoi* is the most abundant species, biomass of *P. minutus* usually exceeds *P. lozanoi* biomass. This can be explained by the size difference between the two species: *P. minutus* averaged 57 ± 9 mm standard length, *P. lozanoi* averaged 37 ± 7 mm standard length (all samples taken together).

Food resource utilisation at locality 4 (Fig. 9.4), expressed as gravimetric percentage, was quite constant over a wider size range (40-55 mm) than used for the intercomparison of the different localities. Both species depended mainly on *Schistomysis spiritus* and *Atylus swammerdami* but in almost exactly opposite proportions.

Table 9.1. Number of stomachs examined in the 45-50 mm size class (N stomachs), number of prey items found (N items) and average Fullness Index (FI) for both species at the 5 selected localities.

Locality	1	2	4	5	10
Pomatoschistus minutus					
N stomachs	10	20	20	20	19
N items	488	154	299	217	199
FI	0.2	2.9	1.1	2.8	0.8
Pomatoschistus lozanoi					
N stomachs	10	20	20	20	18
N items	72	64	112	219	91
FI	0.1	1.8	1.7	4.4	1.1

Basic data on the stomach analyses are given in Table 9.1. Food composition of both species at the different localities, expressed as gravimetric %, is summarised in Fig. 9.5. In *Pomatoschistus minutus* diet differed considerably at the different localities (Fig. 9.5), but mysids were always important (>15%). At locality 1 *Schistomysis kervillei* dominated, but this is due to a single large *S. kervillei*. Polychaetes, mainly *Lanice conchilega*, and the small gammaridean amphipod

Microprotopus maculatus were of subsidiary importance.

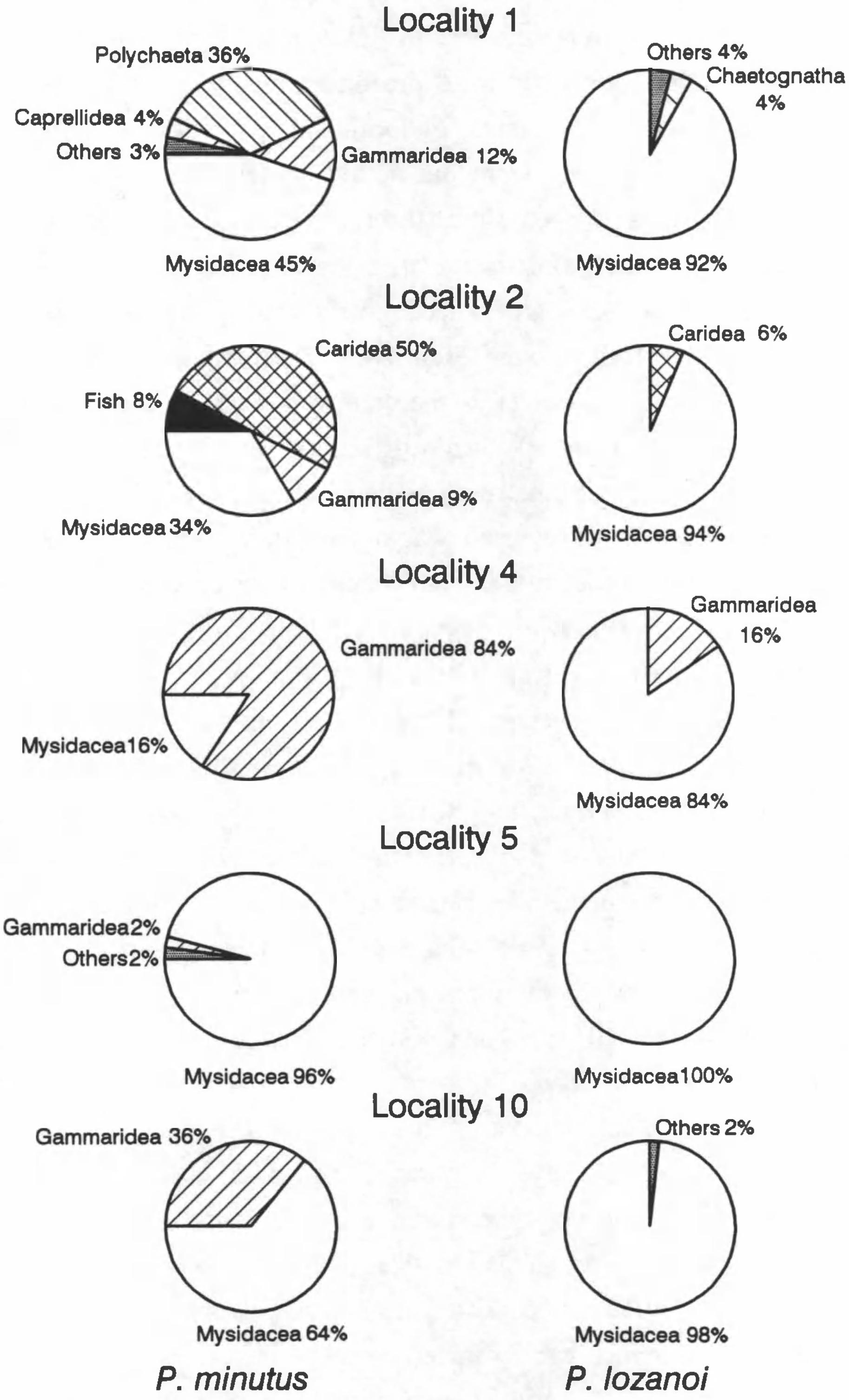


Fig. 9.5. Food composition (%G as ADW) for the 45-50 mm size class of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* at the 5 selected localities.

At locality 2 the caridean shrimp *Crangon crangon* was the dominant food item. Strangely these were fragments of shrimp larger than the gobies so presumably the gobies were scavenging on dead shrimp, perhaps undersized cooked shrimp discarded from a commercial trawler. In this locality *Schistomysis spiritus* was the dominant mysid, the amphipods were predominantly *Atylus swammerdami* and the fish concerned a single *P. lozanoi*. In locality 4 gammaridean amphipods, almost exclusively *A. swammerdami* were the dominant item, with some *S. spiritus*. At locality 5 *S. spiritus* was taken almost exclusively. Finally in locality 10 it was *S. spiritus* again plus some *A. swammerdami*.

Pomatoschistus lozanoi depended nearly exclusively on mysids at all sites (>80%). In locality 1 these were exclusively *Schistomysis spiritus*, in spite of the fact that the heavier *S. kervillei* was the dominant mysid in the hyperbenthos at the site. At localities 2, 4, 5 and 10 *S. spiritus* was by far the dominant item. At locality 4 this was supplemented with *A. swammerdami*.

In numerical terms the result was quite different (Fig. 9.6) especially at the inshore sites, indicating that more small items, which contributed little to the %G, were taken there. At locality 1 *P. minutus* consumed large numbers of *Dactylopusia vulgaris*, a harpacticoid which, in the stomachs, occurred between the radiole crowns of *L. conchilega* together with the small amphipod *M. maculatus* and the caprellid *Pariambus typicus*. At locality 2, besides *S. spiritus* and *A. swammerdami*, *D. vulgaris* was still important (now without *Lanice*) together with a variety of small amphipods, mainly *Pontocrates altamarinus*. At locality 4 *A. swammerdami* was by far the most important item. The harpacticoids were still mainly *D. vulgaris*, but also some *Halectinosoma sarsi* and *Euterpina acutifrons*. In locality 5 *S. spiritus* and some *A. swammerdami* were supplemented by the calanoid copepod *Temora longicornis*. In locality 10 *A. swammerdami* and *S. spiritus* dominated again, with some *Gammarus crinicornis* and *S. kervillei*.

P. lozanoi also consumed a lot of *M. maculatus* and *D. vulgaris* at locality 1. The mysids were exclusively *S. spiritus*. Calanoid copepods were mainly *T. longicornis* but also *Centropages hamatus*. *P. lozanoi* also consumed *P. typicus* and radiole crowns of *L. conchilega*, besides the chaetognath *Sagitta elegans*. At localities 2, 5 and 10 the diet consisted almost exclusively of *S. spiritus*. At locality 4 its numerical importance was swamped by numerous *A. swammerdami*. In locality 10 *A. swammerdami* and *S. kervillei* supplemented the *S. spiritus* diet.

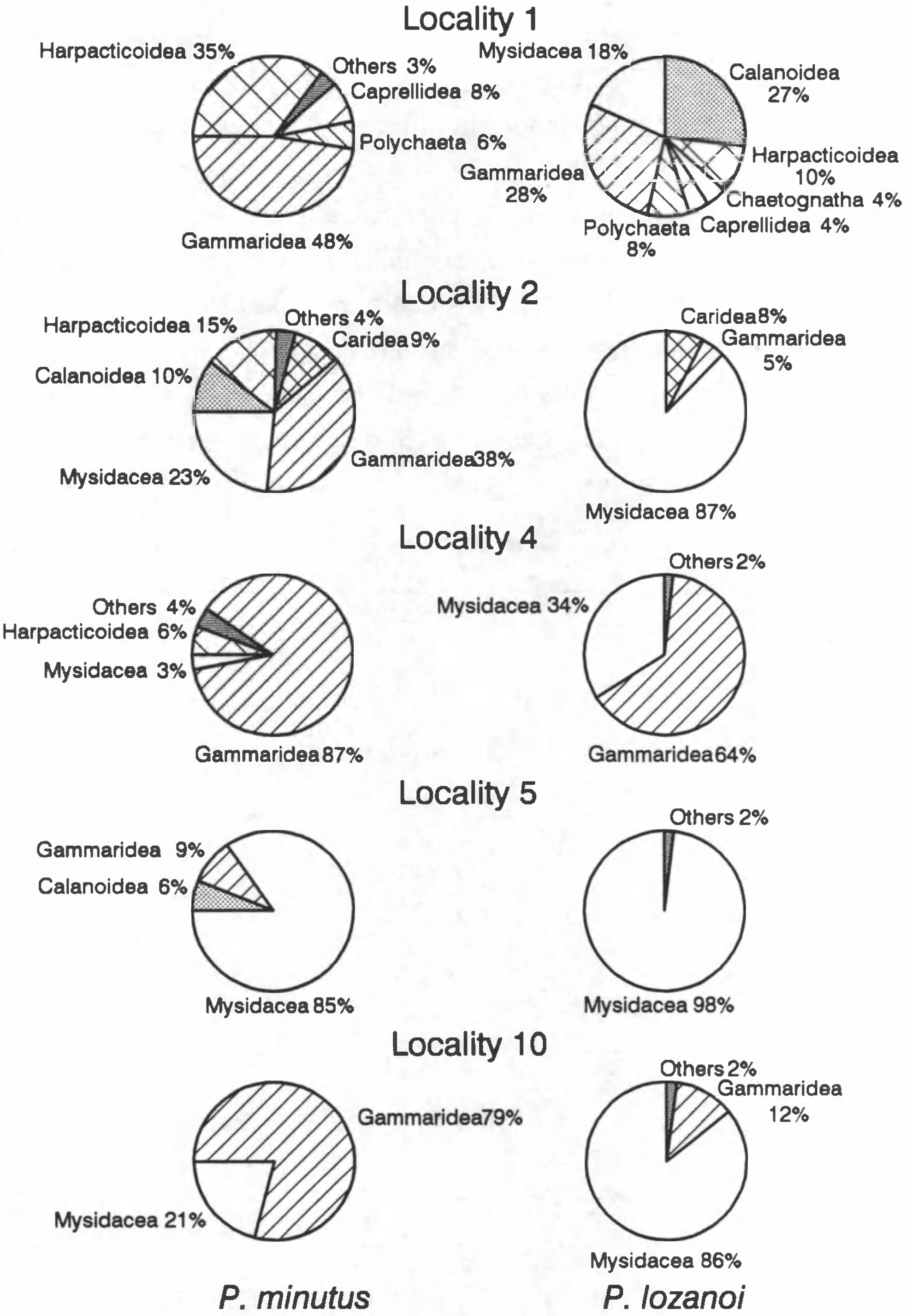


Fig. 9.6. Food composition (%N) for the 45-50 mm size class of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* at the 5 selected localities.

The FI (Table 9.1, Fig. 9.7), a measure of feeding intensity, of *P. minutus* at locality 1 was significantly lower than at the other localities ($p < 0.005$ or better), except for locality 10 ($p = 0.01$, N.S.). FI among localities 2 and 5 and among localities 4 and 10 were not significantly different ($p = 0.8$ and $p = 0.2$, respectively), but they were significantly different among the mixed pairs of these ($p<0.005$). The FI of *P. lozanoi* at locality 1 was significantly lower than at all other localities ($p<0.001$). At locality 5 FI was significantly higher than at the other localities ($p<0.001$). There were no significant differences between the FI of *P. minutus* and *P. lozanoi* at any locality ($p>0.01$).

Basic data on goby biomass, prey biomass and relative food abundance are given in Table 9.2. When the Renkonen index for the gravimetric data is plotted in relation to relative food abundance at the different sites (Fig. 9.8) it is obvious that, both for hyperbenthic relative food abundance (Fig. 9.8a) and for macrobenthic relative food abundance (Fig. 9.8b), there is no increasing trend of resource overlap with relative food abundance. Only in locality 1, where relative food abundance was lowest, resource overlap was very small.

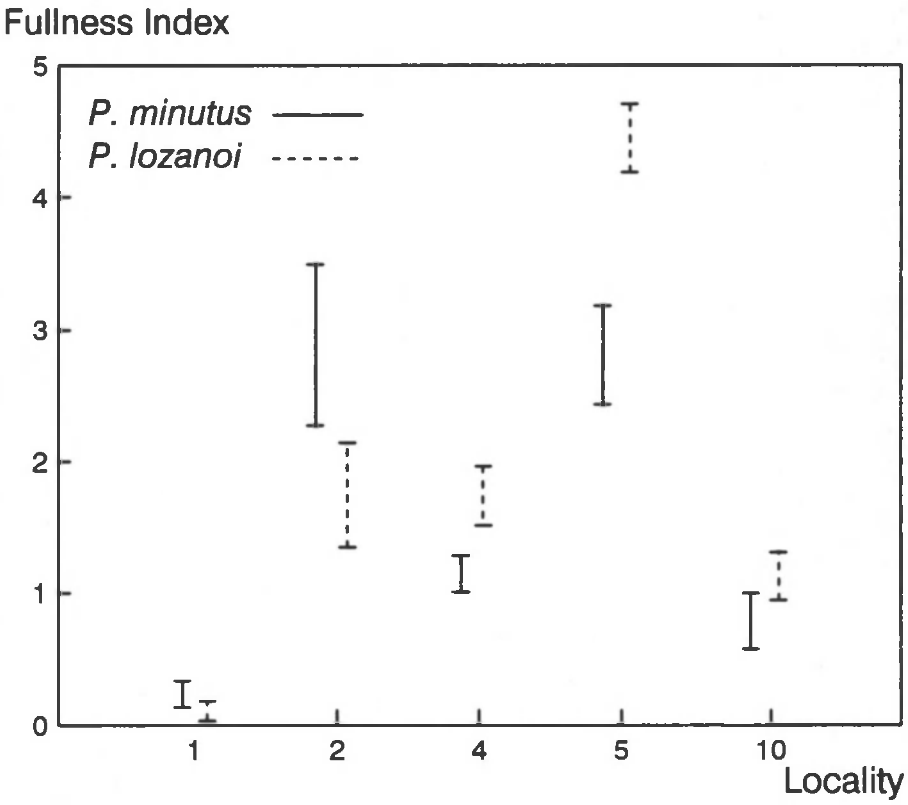


Fig. 9.7. Average FI (± 1 standard deviation) for the 45-50 mm size class of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* at the 5 selected localities.

For the hyperbenthos in the other localities there seems to be an opposite trend with decreasing resource overlap at the highest relative prey abundances (Fig. 9.8a). In the plot of the Renkonen overlap against macrobenthos relative prey abundance (Fig. 9.8b) no trend can be observed.

Table 9.2. Biomass of both goby species (g ADW per 1000 m^2), biomass of hyperbenthic prey (g ADW per 1000 m^2) and macrobenthic prey (g ADW per m^2) present and food resource overlap as measured by the Renkonen index, both gravimetrically and numerically at the 5 localities where stomachs were analysed.

Locality	1	2	4	5	10
Pomatoschistus minutus	3460	15	14	10	15
Pomatoschistus lozanoi	390	51	16	9	9
Hyperbenthos	17	19	7	0.7	4
Macrobenthos	82	33	4	2	8
Renkonen gravimetric	0.03	0.40	0.30	0.96	0.59
Renkonen numerical	0.44	0.34	0.68	0.85	0.31

Using the numerical overlap index (Fig. 9.9) no correlation can be detected for either hyper- (Fig. 9.9a) or macrobenthic relative prey abundance (Fig. 9.9b) and resource overlap seems to be independent of relative food abundance.

DISCUSSION

Competition can be defined as the negative effects which an organism has upon another by consuming, or controlling access to, a resource that is limited in availability (Keddy 1989). One of the possible consequences of interspecific competition is that the species will partition resources when co-occurring, i.e. that their fundamental niche, the pattern of resource use documented in the absence of heterospecific neighbours, will be contracted to a realised niche. Resource partitioning in fish was recently reviewed by Ross (1986). In his definition resource partitioning was taken to mean any substantial difference in resource use by coexisting species, independent of the underlying causal mechanisms. Originally, the concept of resource partitioning was developed in relation to the evolutionary change in species in response to selection pressures generated by interspecific competition (Walter 1991). As ecology is already overburdened with terms that have many meanings (and consequently risk having no meaning at all), the use of resource partitioning should perhaps be restricted to its original meaning (Walter 1991). In the present study difference in resource use is suggested as a replacement term of the wider concept used by Ross (1986).

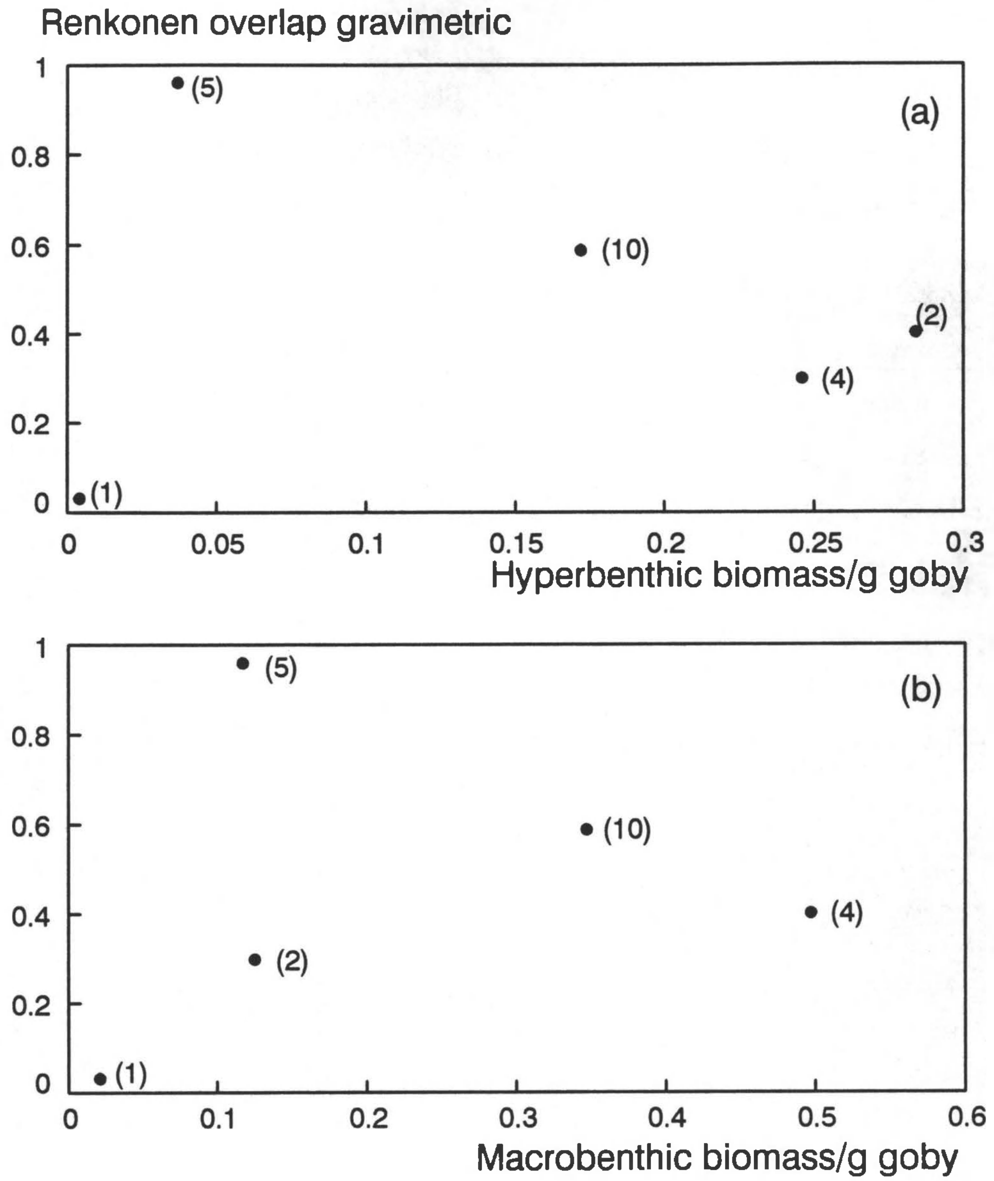


Fig. 9.8. Renkonen gravimetric overlap between *Pomatoschistus minutus* and *Pomatoschistus lozanoi* plotted against hyperbenthic (a) and macrobenthic (b) relative food abundance at the 5 selected localities.

The study of competition is not one of the fields in which ecologists have shown the most restraint in jumping from simplistic results to far-reaching conclusions. Even if present day competition is rare and impotent in natural systems there are indications that it is particularly strong among, mostly North-American, ecologists. Some of the controversy in the literature is pure mud-throwing and papers responding to harsh criticisms may start with a few pages of philosophy and semantics (e.g. Roughgarden 1983, Simberloff 1983). When ecologists turn to philosophy and semantics for resolving their disputes it is usually a sign that the data do not speak for themselves. Some scientists see hopeful signs in the mud-throwing chaos as, to them, it signals the advent of a new paradigm in ecology (see Price *et al.* 1984), which says perhaps more about the Messianic beliefs of scientists than about their grasp of the structure of scientific revolutions (Kuhn 1970).

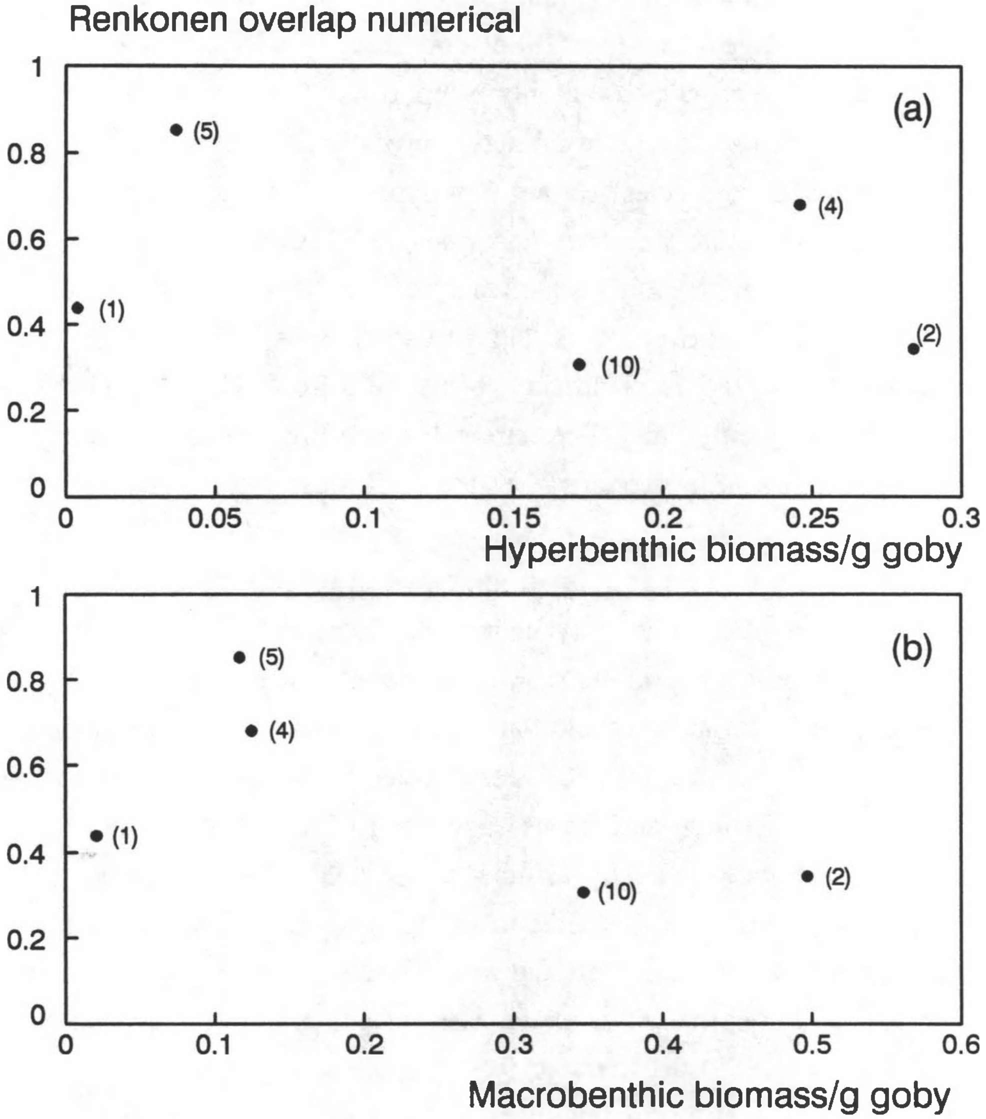


Fig. 9.9. Renkonen numerical overlap between *Pomatoschistus minutus* and *Pomatoschistus lozanoi* plotted against hyperbenthic (a) and macrobenthic (b) relative food abundance at the 5 selected localities.

Many studies claiming to demonstrate interspecific competition can be simply discarded on the basis of faulty logic and/or superficial reading of the literature. For example, in the marine fishes literature the erroneous notion exists that, if some overlap measure is higher than a certain threshold value, this is 'significant', from which some authors then conclude that competition occurred (e.g. Thorman 1982;

Le Mao 1986; Harmelin-Vivien *et al.* 1989; Warburton & Blaber 1992). Thorman (1982) neatly avoids making any explicit statement on threshold values and emphasises that, in the absence of data on food availability, it is impossible to test for competition. However, from high overlap values and changes in niche width, he still concludes that competition for food affects the interactions between the fish species in his assemblage. Le Mao (1986) conveniently uses an index that is not stated nor explained, and which is only supported by grey literature. He then concludes that 'largely as a result of an active predation responsible of interspecific competition between these species' certain prey types 'suffer massive mortalities ...', a cryptic phrase if ever there was one. According to Harmelin-Vivien *et al.* (1989) a Renkonen overlap value of 0.6 is significant, a statement for which reference is made to Keast (1978). However, Keast (1978) used Levins' (1968) index and stated that an overlap of over 0.7 is significant. Moreover, Keast (1978) explicitly states that this significance is only valid if resources become limiting and he always refers to 'potentially significant' overlaps as the resource base was known only qualitatively. Strangely, in the results section Harmelin-Vivien *et al.* (1989) state that interspecific competition was very strong between juveniles but in the discussion section it is said that 'dietary identity in juvenile Scorpaenidae does not imply the existence of competition for food, as their prey are extremely abundant'. Warburton & Blaber (1992) attribute the threshold value of 0.6 for the Renkonen index (which, like Harmelin-Vivien *et al.* (1989), they refer to as the Schoener index) to Zaret & Rand (1971). However, these authors use a version of the Morisita index modified by Horn (1966) and state that they assume a threshold value of 0.6 is significant overlap. Warburton & Blaber (1992) are a bit more careful in their conclusions where they state that, because of the high overlap values found, scope for competition existed among members of the assemblage. They refer to a statement by Holbrook & Schmitt (1989) that overlap 'can be both a cause and a consequence of competition'. This is a confusing statement as competition is normally perceived as being a process, which can hardly be the consequence of overlap, which refers to an observation. Incidently, Holbrook & Schmitt (1989) use a Proportional Similarity Index, which is again the Renkonen (1938) index, for which they refer to Feinsinger *et al.* (1981), who use it as a measure of niche breadth by calculating the overlap between selected prey and prey available in the environment. Feinsinger *et al.* (1981) in turn attribute the index to Czekanowski (no reference). The notion of a threshold value in resource overlap stems from the desire to equate simple measures of resource overlap, such as the Renkonen index, with the competition coefficients in a set of Lotka-Volterra equations, a notion defended as recently as 1983 by

Schoener (1983). Measurement of the competition coefficients requires detailed study of the population dynamics of each species at different relative abundances in relation to a known carrying capacity.

As was already pointed out by Colwell & Futuyma (1971) there is no simple relationship between the degree of resource overlap and the existence of competition in the absence of data on food availability. As this notion seems not to have been taken up by at least part of the scientific community, a summary of the logic of the argument is repeated here. A complete resource overlap may occur in the absence of competition when food is overabundant. At the other extreme a completely different resource use or zero overlap may be a strong argument for the existence of competition if food is limiting.

Deciding which prey are available to the predator in field studies of complex and diverse environments is extremely difficult (Connell 1980). Therefore the very cogent arguments of Hurlbert (1978) against the use of the Renkonen index and his desire to replace it by an index taking into account the frequency of interspecific encounter and the abundance of each resource state (or prey species availability) are not helping the field ecologist very much further. The main difficulty lies in distinguishing between what prey is available in comparison to what is present, or stated differently, in distinguishing food availability from food abundance. For some prey items acceptable subjective assessments can be made, i.e. a large *Mya arenaria* is unavailable to a small goby. In fishes depending wholly or partly on infaunal animals, it is nearly impossible to know what percentage of a certain prey type is available at a certain point in time. More research into the emergence behaviour of burrowing animals is clearly warranted. The use of sophisticated underwater camera systems that do not need artificial light for operation is a distinct possibility. Direct observations could possibly also demonstrate that a different usage of microhabitats is really underlying the difference in food resource use. For example, the preference for *Atylus swammerdami* in *P. minutus* as opposed to the preference for *S. spiritus* in *P. lozanoi* in locality 4 may simply be due to *P. minutus* foraging around colonies of Bryozoan and Hydrozoans, where high densities of *A. swammerdami* occur (Cattrijsse *et al.* in press). With regard to the emergence behaviour, the interpretation of the simple test in the present study is not without difficulties. In the present study the implicit assumption was made that the emergence behaviour of benthic prey, and therefore the fraction of it that was available to the gobies, was constant over the different habitats. This is unlikely to be true as the faunal composition varies between habitats (Hamerlynck *et al.* 1992) and that the emergence behaviour of amphipods, the dominant infauna of the poorer habitats, is not necessarily similar to the emergence behaviour of polychaetes, one of the dominant potential prey in the richer habitats.

Even when authors have been able to know density, biomass, and production of predators and prey quite accurately and even when they have been able to make fairly acceptable subjective estimates of prey availability, the choice of conversion factors for the calculations of consumption can result in completely opposite statements on food-limitation (and therefore competition) in adjacent and very similar habitats. Evans (1983) estimated that an assemblage of epibenthic predators exported 17 to 20 % of benthic biomass production from Kvarnbukten Bay and concluded they were probably not competing as the resource did not seem to be limiting. According to Pihl (1985) the same predator guild consumed 98 % of the annual production of *Corophium volutator*, 92 % of 0-group *Cerastoderma edule* production and 62 % of 0-group *Mya arenaria* production and therefore competed for food in an adjacent bay. The estimates by Evans (1983) and Pihl (1985) of meiofauna consumption were similarly incompatible (Gee 1989). Evidently some basic work on conversion factors for different groups is still needed before studies, claiming to compare prey availability and food consumption in small demersal fish and epibenthic invertebrates, can be used for the study of interspecific competition.

According to the classification of Keddy (1989) the present study is a snapshot comparative study which investigates pattern along a gradient. In comparison to field experiments the disadvantage is that a process, namely competition, is inferred from a pattern. Many factors have implicitly been assumed to be constant at all localities. The emergence behaviour was already mentioned. Catchability is another one: water transparency in the Voordelta increases with distance from the shore (Mees & Hamerlynck 1992) and net avoidance by gobies, mysids and amphipods may therefore vary accordingly. Other potential sources of bias are the patchiness of the hyperbenthos: the abundance on one side of the vessel may not accurately reflect the abundance some 15 meters away where the fish were actually feeding.

Theoretically, carefully planned and well executed manipulative field experiments (e.g. Schmitt & Holbrook 1990) can be used to assess if competition is the mechanism causing interspecific differences in resource use. However, field experiments involving removal and/or addition of one species may be logistically very demanding or simply impossible to perform in some of the commonest natural habitats. The generality of the findings, when doing these experiments in a selected habitat, where manipulation is easier, may be questioned (Keddy 1989).

The prediction which follows from the hypothesis under consideration is that the difference in resource use, that should follow from interspecific competition, will be stronger in areas of food-limitation than in areas of high food abundance.

Evidently, both species have considerable plasticity in their food resource use and in general there seems to be no decrease in resource overlap in the poorer sites, except for locality 1. Moreover, neither species was feeding very actively at this locality, or at least not taking many large items, and, to someone biassed towards finding competition (see Keddy 1989), this observation might be interpreted as strengthening the case for interspecific competition. However, Fullness Index is merely a measure of the size of the recent meal. In biomass terms both species indeed had a very low overlap in locality 1, *P. minutus* food being dominated by *Schistomysis kervillei*, *Lanice conchilega* and *Microprotopus maculatus* and *P. lozanoi* concentrating on *Schistomysis spiritus*. However, this overlap measure became biassed precisely because of the low feeding intensity, a single *S. kervillei* dominating over the 487 other items in *P. minutus*. In numerical terms overlap was similar to the overlap measured at the other sites and so the case for interspecific competition is considerably weakened. The lull in feeding activity may have been only temporary. In all localities both species seem to be feeding (or fasting) in concert. It is perfectly unclear what may have been the cause of the strong differences in feeding intensity observed, without more knowledge on prey activity (see also Hamerlynck *et al.* submitted a). Perhaps the feeding activity of one species is even beneficial to the other species, e.g. in locality 4 *P. minutus* may be able to catch more *Gammarus crinicornis* because the amphipods react in some way to the presence of actively feeding *P. lozanoi*, and vice-versa for *Schistomysis spiritus*. This type of behaviour is well known in birds of prey, where species using different strategies e.g. the hobby *Falco subbuteo* and the hen harrier *Circus cyaneus*, may hunt cooperatively. The image of the hunting falcon makes birds settle on the ground as a hobby usually takes its prey in flight, thus they are easy prey for the harrier, which pounces on prey on the ground. Conversely birds that see the harrier first try to escape by taking wing, only to fall prey to the hobby.

Whatever the causes for the aberrant FI and low overlap in gravimetric terms in locality 1, the absence of a clear trend in resource overlap in relation to the inferred measure of prey abundance seems to imply we have to reject H_1. Therefore interspecific competition for food is unlikely to be the mechanism that caused the observed differences in resource use in the size class of gobies investigated.

An alternative hypothesis is that interspecific competition has been a selective force in a distant past which has led to character displacement in the two species. The size difference between the two species is a case in point. For similar sized animals of the two species a further difference may lie in the morphodynamics of the jaw apparatus (Barel 1983, Aerts 1992), *P. minutus* being better adapted for biting and *P. lozanoi* being better adapted for suction feeding. This is illustrated by the difference in food resource use observed at locality 2 where, in comparison to *P. minutus*, *P. lozanoi* hardly fed from the dead shrimp, which presumably requires biting. Also in the Belgian coastal waters *P. lozanoi* only rarely took items which require biting, such as bivalve siphons and radiole crowns of *Lanice conchilega* (Hamerlynck *et al.* 1990), which were very important for *P. minutus* (Hamerlynck & Cattrijsse submitted). Still, preliminary studies of *P. minutus* and *P. lozanoi* morphology do not show any obvious anatomical differences between the oral jaw apparatus of both species (P. Aerts & D. Decleyre unpubl. data). Both have relatively unspecialised jaws that can be used in both feeding modes (D. Decleyre unpubl. data), biting and suction feeding. However, more subtle differences may exist in the muscular dynamics.

ACKNOWLEDGEMENTS

Colin Janssen, Rik van Landtschoote and Peter van de Vyver participated in the field sampling. The research was partly subsidised by the Dutch Rijkswaterstaat, dienst Getijdewateren Middelburg and the Belgian FKFO project 32.0086.88. Sampling was greatly facilitated by the seamanship and help of W. Röber, C. van Sprundel, P. de Koeyer, H.W. Francke and G. Desmet.

Chapter 10

Growth, feeding, production and consumption in 0-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow coastal area of the SW Netherlands

Hamerlynck, O. & Hostens, K. 1993. Growth, feeding, production and consumption in 0-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow coastal area of the SW Netherlands. ICES Journal of marine Science 50: 81-91.

ABSTRACT

In 1988 juvenile bib *Trisopterus luscus* and whiting *Merlangius merlangus* were studied in a shallow coastal area by monthly sampling with fine meshed nets. 0-group fish of both species are first caught in May. By the end of the first growth season bib reached about 150 mm SL (Standard Length), whiting about 170 mm SL. Maximal densities were recorded in June and by the end of the year most fish had left the area. The instantaneous mortality is estimated at 0.008 day^{-1} (0.77 % day^{-1} for bib and 0.76 % day^{-1} for whiting) for both species. In May both species depended almost exclusively on calanoid copepods. In June and July mysids and amphipods were the most important invertebrate prey, but small fishes such as gobies provided a substantial proportion of the energy requirements, especially in whiting. From August onwards shrimp and fish dominated the diet in both species. Using Jones' (1974) model, food consumption as % body weight day^{-1} varied between 4 and 6 % during summer and declined to 2 to 3 % in autumn. Total consumption per unit area of subtidal seafloor, by the 0-group fish of both species taken together, was estimated at 0.47 g Ashfree Dry Weight (ADW) m^{-2} yr^{-1} using Jones' (1974) model and at 0.57 g ADW m^{-2} yr^{-1} using a conversion efficiency (P:C ratio) of 0.34.

INTRODUCTION

0-group bib *Trisopterus luscus* and whiting *Merlangius merlangus* are an important ecological component of estuaries (Claridge & Potter 1984), marine bays (Hostens & Hamerlynck in press) and shallow coastal areas (Redant 1977). Bib are not landed in great quantities in the North Sea but are commercially important in France (Desmarchelier 1985b), Portugal (Sobral & Rebordão 1982) and Spain (Benvegnú 1971). Whiting are of considerable commercial importance (Hislop & MacKenzie 1976) and rank second in weight terms in groundfish surveys in the central, southern and eastern North Sea (Daan *et al.* 1990).

Data on the food of larval bib and whiting, to a size of 11 mm, in the southern North Sea are given in Last (1978). Information on the food of bib of less than 130 mm is needed, but cannot be obtained from commercial catches (Santos 1989). Some data exist on the food of 0-group bib in the Irish Sea (Nagabhushanam 1965, Armstrong 1982), the Loire estuary (Robin & Marchand 1986), the Medway (Broek 1978) and the Elbe (Kühl 1973). There is also some 'grey' literature on the subject (e.g. Gherbi-Barre 1983, Puente 1986). For 0-group whiting there are data from Icelandic waters (Pálsson 1980), the Scottish west coast (Gordon 1977b), the Irish Sea (Nagabhushanam 1965), the northern North Sea (Robb & Hislop 1980, Robb 1981) and the Medway estuary (Broek 1978). A very extensive report on the food of whiting in the North Sea is given in Hislop *et al.* (1991) but the smallest size class covered in that study is 100 to 149 mm total length. This size class corresponds to 0-group only for the last quarter of the year.

In order to fill the gap in the knowledge on food consumption by bib and whiting, 0-group fish were collected using fine meshed nets in a shallow coastal nursery area during 1988.

MATERIALS AND METHODS

Study area

The study area proper covers the central part of the Voordelta (Fig. 10.1a) which is the shallow coastal area formed by the interlinked ebb tidal deltas of the (former) estuaries of the Dutch Delta where three main European rivers, the Rhine, the Meuse and the Schelde, enter the North Sea. The Voordelta stretches from the Belgian-Dutch border in the south to the Hoek van Holland in the north. Its marine boundary is arbitrarily defined by the depth contour of 10 m below Mean Tidal

Level (MTL) as defined for Amsterdam, which is at 10 to 15 km seaward from the coastline. A detailed description of the hydrodynamics and geomorphology of the Voordelta is given in Louters *et al.* (1991).

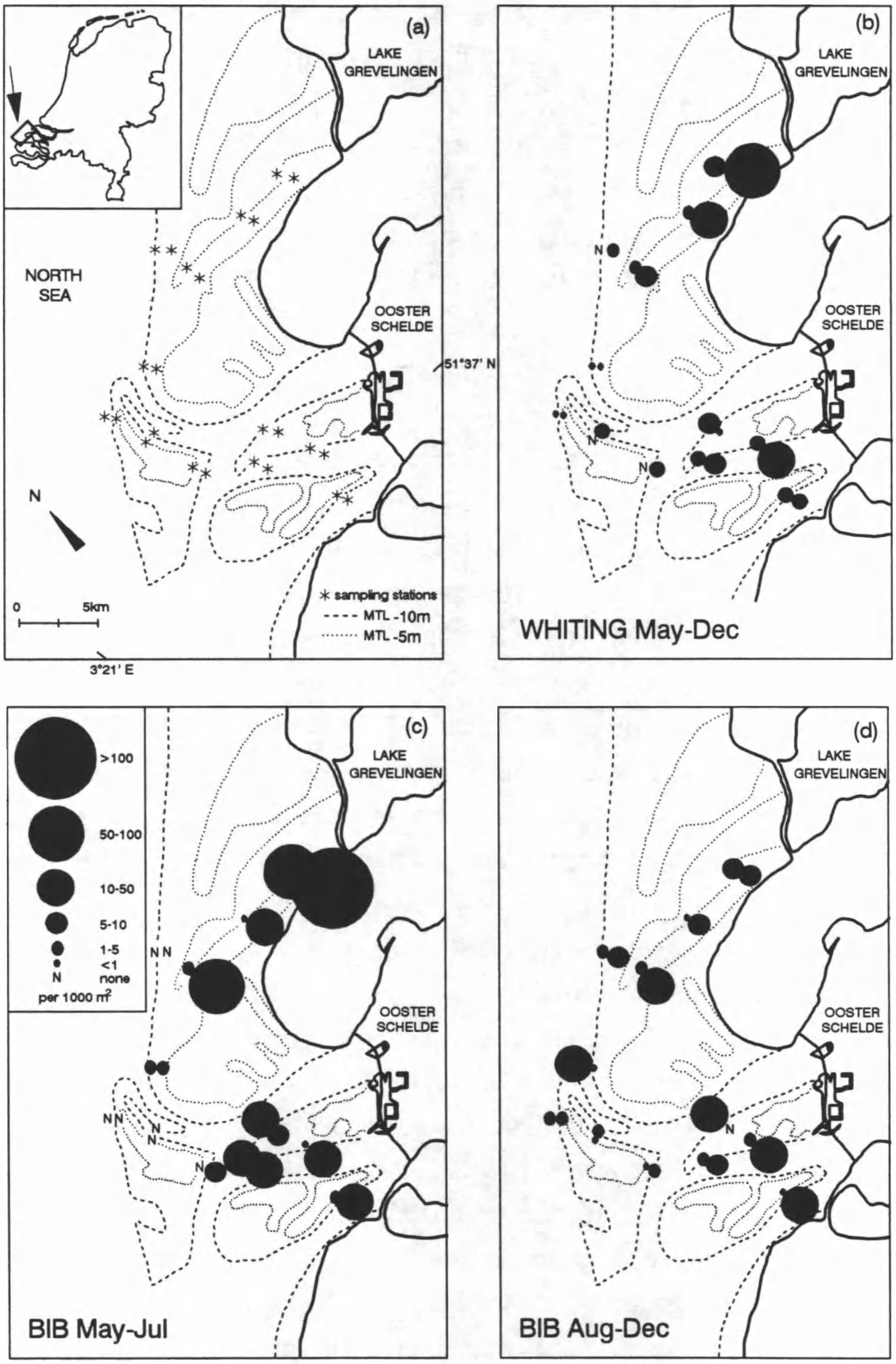


Fig. 10.1. Map of the study area (a, sampling stations; b, distribution of whiting mean densities; c, distribution of bib mean densities from May through July; d, distribution of bib mean densities from August through December). MTL is the Mean Tidal Level as defined for Amsterdam.

The area was greatly affected by the engineering works which were undertaken to protect Zeeland from disastrous storm surges (Louters *et al.* 1991). In relation to these engineering works the benthic ecology of the area has been quite extensively studied: meiofauna (Heip *et al.* 1990, Vanreusel 1990, 1991), macrofauna (Craeymeersch *et al.* 1990) and hyperbenthos (Hamerlynck & Mees 1991, Mees & Hamerlynck 1992).

The spatial structure of the fish and mobile epifaunal assemblages in the area is discussed in Hamerlynck *et al.* (in press). The area is a nursery for flatfish, especially dab, sole and plaice (Hamerlynck *et al.* 1992). Data on the parasites of juvenile gadoids in the area will be published elsewhere (Damme *et al.* in prep.).

Sampling

During 1988 monthly samples were taken at twenty-four stations in the Voordelta (Fig. 10.1a). These stations cover two depth strata (5 m below MTL and 10 m below MTL) at 12 localities. Samples were taken from the R.V. "Luctor" (34 m, 500 Hp) using a 3 m beam trawl, equipped with a 6 m long shrimp net with a 5x5 mm mesh in the cod end, a tickler chain and a chain in the groundrope. Hauls were 1 km in length, starting from a buoy or other fixed marker, the distance covered being read from the radar screen. Ship speed relative to the bottom when trawling was about 4.5 knots. All bib and whiting were anaesthetised in a Benzocaine solution in sea water, to avoid unnecessary suffering and to prevent regurgitation of the stomach content, and were preserved in 7% neutralised formalin. For gadoids of over 70 mm the abdominal cavity was opened to allow rapid fixation of stomach contents. Standard Length (SL), which is a more accurate measure than Total Length (TL) e.g. in case of fin lesions, was recorded for all fish specimens. As in fisheries research TL is the most commonly used measure, linear regressions were calculated between SL and TL for a size range of both species. When comparing the results from the present study with studies using TL, the TL measurements were first converted to SL. Biomass was calculated from length - Ashfree Dry Weight (ADW) regressions. Ashfree Dry Weight (ADW) was measured as the difference between dried (60°C for 5 days) and ashed (550°C for 2 hours) weights of a size range of both species. Net efficiency, the number of 0-group gadoids caught in comparison to the number actually present per fished unit area of subtidal seabed, was assumed to be 20 % for all size classes of fish. This point is taken up in the discussion. Densities were calculated as N 10^{-3} m^{-2}, biomass as g ADW 10^{-3} m^{-2}. For conversion to numbers caught 10^{-3} m^{-2}, densities have to be divided by 5. For conversion to numbers caught h^{-1} of trawling no exact factor can be given. Although the hauls were 1 km in length, haul duration depended on current velocity, wind speed and direction and wave action but, by multiplying the reported densities by 4.4, the number of fish caught h^{-1} can be approximated.

A Wilcoxon signed rank test on pairs of variables was performed, comparing the densities of the individual 5 m and 10 m depth hauls for each locality, to test for depth preference of bib and whiting.

Stomach analysis

For each month 15 to 20 individuals of each species were selected at random for stomach analysis. Because of the low number of stomachs examined for November and December data were pooled for these months. In total 97 bib and 101 whiting stomachs were analysed. All items in the stomach were identified, if possible to species level, and measured. The original ADW of the prey, prior to ingestion was calculated from length-ADW regressions obtained for prey from the same area (Appendix). Prey importance is expressed both numerically and gravimetrically. Dry weight of the stomach content (110 °C for 2 to 4 h) was measured for the calculation of the Fullness Index (FI) (Berg 1979). For statistical purposes FI was arcsin-transformed (Sokal & Rohlf 1981). About 80 % of the fish found in the stomachs could be identified, at least to genus level, by comparing skeletal elements to a reference collection. Unidentified fish were apportioned in accordance to the numerical or gravimetric percentages of the identified ones (Hislop *et al.* 1991). The diversity of the diets of both species, a measure of niche breadth, was calculated as Shannon-Wiener H' (Washington 1984):

$$H' = -\sum_{i} p_i \log p_i$$

where p_i is the proportion of the number prey of the i^{th} species in the diet over the total number of items in the diet.

Growth, mortality, production and consumption

Growth is measured as the increase of mean length of 0-group fish per month. The instantaneous mortality rate Z is defined as the decrease in density of 0-group fish in the study area and is calculated from the linear regression equation fitted through the ln transformed densities (bib: June through December; whiting:

June through October).

Total production P of the cohort over the time period considered is:

$$P = \sum \Delta P$$

where the monthly production ΔP can be estimated as:

$$\Delta P = \frac{N_t + N_{t+\Delta t}}{2} \Delta \overline{w}$$

where N_t is the density at time t and Δw is the mean growth increment for this month (Crisp 1984).

Food consumption was estimated directly from the stomach content data using Jones' (1974) model. This model estimates the stomach evacuation rate r (in g h^{-1}) from

$$r = S^{0.46} * (L/40)^{1.4} * Q * 10^{0.035(T_0 - T_c)}$$

with S the average weight of the stomach content (g wet weight), L the total length of fish in cm, Q the rate of evacuation for a 1 g meal of a stated food type of a 40 cm fish at temperature T_c and T_0 the temperature of the sea water when sampling. Patterson (1985) gives an erroneous formulation of the same model with *40/L* instead of *L/40*. It seems probable that Patterson's calculations have been done with the correct formula, though this cannot be verified from the paper. For use in the model, ADW measurements were multiplied by 5 in order to convert to wet weight. After the calculations they were converted back to ADW. Judging from stomach fullness data in Robin & Marchand (1986) bib feed at about the same rate throughout a 24 h cycle. Similarly Gordon (1977b) finds little variation in whiting stomach fullness over 24h. Patterson (1985) reports an early morning peak and an evening dip in stomach fullness of whiting. Around noon stomach fullness is average. Robb (1981) finds a two-peaked feeding periodicity in whiting. One of the peaks is around midnight, the other around midday. As both peaks are of the same magnitude stomach content weights of fish collected during daylight hours can be assumed to be representative for the entire 24h. For the fish part, of the stomach content, a Q-value of 0.26 was used and, for the crustacean part, a Q-value of 0.19 (Jones 1974). The latter value was also used for the rarely consumed non-crustacean invertebrates.

Assuming equilibrium between intake and consumption, the daily food intake C could be calculated:

$$C = r * 24$$

where r is the stomach evacuation rate as estimated from Jones' model. Daily food intake C is then expressed as φ, the daily feeding coefficient or the percentage of its body weight the average 0-group fish consumed on that sampling date. For bib φ was also calculated according to Pennington (1985), i.e. applying Jones' model to the individual fish and averaging afterwards.

Total (or annual) consumption A over the time period considered is then estimated as:

$$A = \sum_{d=164}^{d=335} \varphi_m \overline{B_d}$$

with φ_m the daily feeding coefficient for the month (or intersampling interval) considered and B_d the average population biomass linearly interpolated between two sampling dates. A P:C ratio or 'ecological efficiency' or 'conversion efficiency' is calculated from production (P) and consumption (A) values. Gross conversion efficiency is the ratio of the growth increment and the reproductive output over food intake. As 0-group gadoids are juvenile, reproductive output can be assumed to be zero and the P:C ratio is equivalent to the net conversion efficiency.

With the partitioning of the food (in weight terms) over the various prey types for each month, the annual consumption of the different prey types is estimated.

Food consumption was also calculated using a P:C ratio of 0.34, as established for 1-group cod by Pihl (1982). According to the data in Jones & Hislop (1978) net conversion efficiencies do not seem to differ substantially between different gadoid species. For whiting Jones & Hislop (1978) report an average P:C of 0.3 but there is a tendency for it to be higher in smaller fish. The 0.34 of Pihl (1982) therefore seems acceptable.

RESULTS

Growth, density and spatial distribution

The observed relationship between Total Length (TL) and Standard Length (SL) was TL = 1.157 + 1.084 SL (N = 111, r^2 = 0.999) for whiting and TL = 2.35 + 1.102 SL for bib (N = 78, r^2 = 0.97). The observed length-weight relationship was ADW = 7.25 10^{-7} $SL^{3.293}$ (N=45, F = 7490, $p < 0.001$) for bib, and ADW = 1.59 10^{-6} $SL^{3.066}$ (N = 47, F = 6124, $p < 0.001$) for whiting.

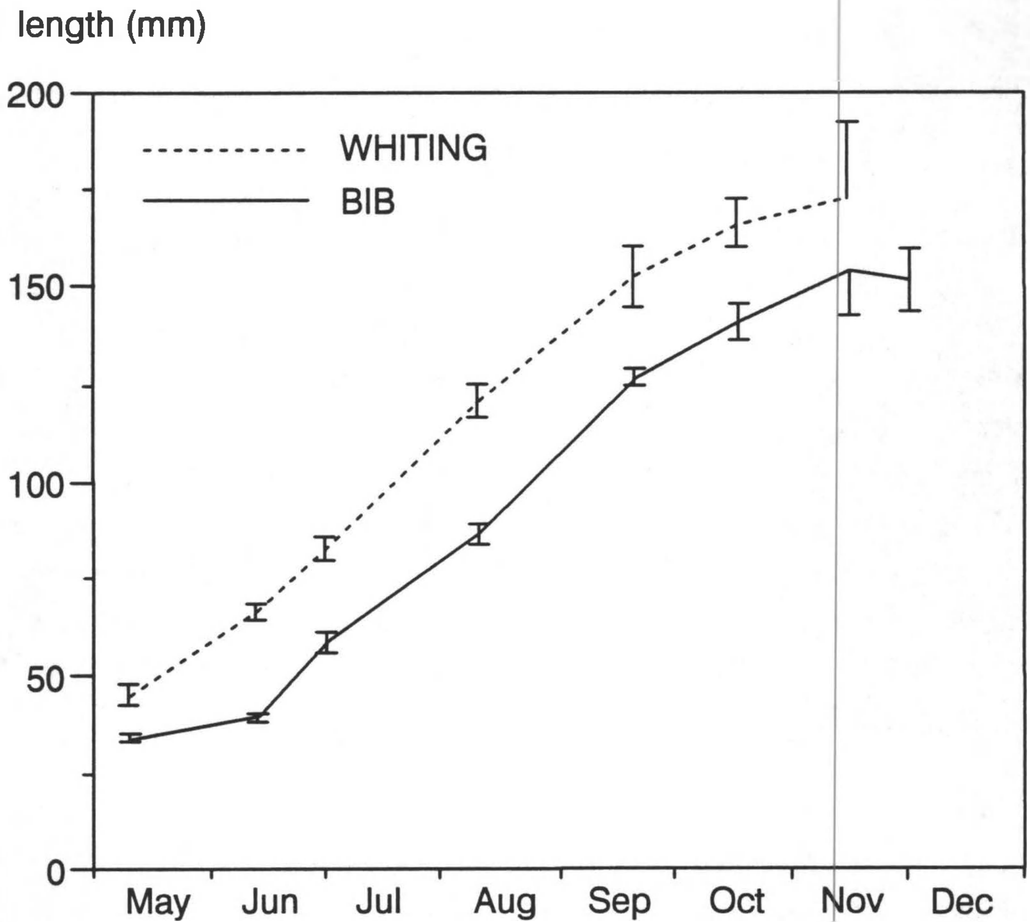


Fig. 10.2. Growth of 0-group bib and whiting: mean standard length per month with standard errors.

The first 0-group bib (N = 5) and whiting (N = 52) were caught in the study area in May, though smaller postlarvae had already been caught with the finer meshed nets of the hyperbenthic sampler (Hamerlynck & Mees 1991) in April (J. Mees unpubl. data). Growth was quite fast with mean lengths of the cohorts increasing from less than 50 mm in May to 154 mm for bib and 173 mm for whiting in November (Fig. 10.2). In December there was a slight decrease in mean length for bib. No mean length was calculated for the two 0-group whiting caught in December.

Table 10.1. Month and daynumber of sample counting from January 1st (d_s), density (N per 1000 m^2) and biomass (g ADW per 1000 m^2) with standard errors for 0-group bib and whiting.

		Trisopterus luscus		*Merlangius merlangus*	
Month	d_s	density	biomass	density	biomass
May	130	0.4±0.3	0.04±0.03	4.6±2.3	0.9±0.4
Jun	164	72.6±52.3	13.3±9.6	28.1±14.7	21.2±11.9
Jul	182	18.1±7.3	11.3±3.8	11.0±4.1	15.2±5.7
Aug	222	11.3±5.8	23.5±14.8	5.8±2.8	23.5±12.4
Sep	263	12.7±4.6	85.8±32.1	3.5±1.1	29.6±10.6
Oct	290	7.0±2.3	68.0±22.5	3.7±1.9	40.0±19.4
Nov	319	1.3±0.5	16.7±7.0	0.2±0.2	2.7±1.9
Dec	335	1.1±0.6	12.6±6.4	0.2±0.1	1.9±1.3

From June onwards bib densities were about double those of whiting (Table 10.1). By November 0-group fish of both species had mostly left the area or had died.

Both species had a strong preference for the 10 m below MTL depth stratum. The Wilcoxon test was highly significant ($p < 0.001$) for both species (bib: $Z = -4.8$; whiting: $Z = -3.6$). There was a clear maximum of abundance in the inner part of the ebb tidal delta of the Grevelingen (Fig. 10.1b and 10.1c). For whiting this remained so throughout the year, for bib the centre of gravity of the distribution shifted towards the ebb tidal delta of the Oosterschelde from August onwards (Fig. 10.1d).

Mortality

The linear regressions fitted through the (ln transformed) densities versus time are highly significant ($r^2_{bib} = 0.94$, $r^2_{whiting} = 0.81$, $p < 0.01$ in both cases) (Fig. 10.3). From these regressions the instantaneous total mortality rate was estimated at 0.0077 day^{-1} (0.77 % d^{-1}) for bib and 0.0076 d^{-1} (0.76 % d^{-1}) for whiting. This corresponds to approximately 21 % $month^{-1}$ in both species.

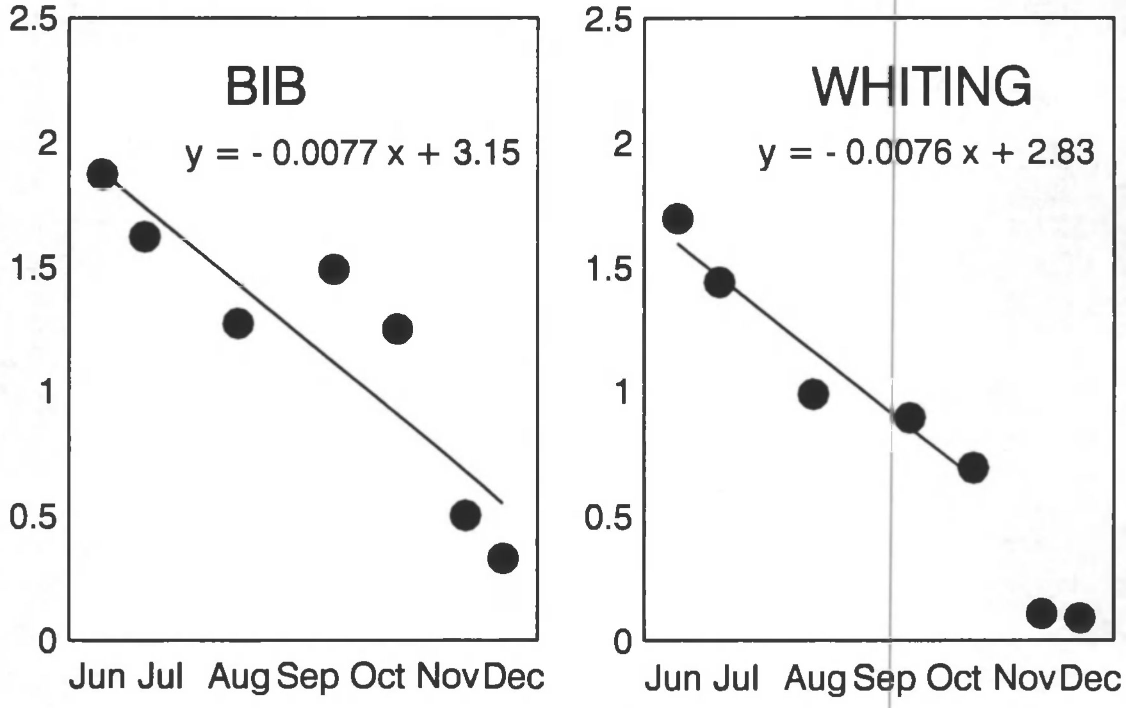


Fig. 10.3. Density of 0-group bib and whiting (ln transformed): means per month with the regression lines for mortality.

Production

Total production per unit area of subtidal seabed for the 0-group (June through December 1988) amounted to 0.13 g ADW m^{-2} yr^{-1} for bib and to 0.06 g ADW m^{-2} yr^{-1} for whiting. The P:B ratio for the time period considered was 4.5 for bib and 3.8 for whiting.

Feeding and food consumption

Average Fullness Index FI (backtransformed) over the study period was 1.75 (s.e. 0.004) for bib and 1.39 (s.e. 0.004) for whiting. Empty stomachs were rare, only three being found in bib and only one in whiting. There was no clear seasonal pattern in the FI (Table 10.2).

Table 10.2. Number of fish caught (N_c), number of stomachs analysed (N_s), mean fullness index with standard error (FI±s.e.), total number of prey items (N_p), daily feeding coefficient according to Jones (φ_j) and according to Pennington (φ_p) for 0-group bib and whiting.

	Trisopterus luscus						*Merlangius merlangus*				
	N_c	N_s	FI±s.e.	N_p	φ_j	φ_p	N_c	N_s	FI±s.e.	Np	φ_j
May	5	4	0.9±0.09	184	-	-	57	17	1.6±0.02	1388	-
Jun	902	21	1.8±0.01	856	4.7	5.1	349	19	1.1±0.03	328	4.2
Jul	234	14	3.3±0.01	247	5.9	6.4	143	17	1.4±0.03	241	4.4
Aug	147	12	1.9±0.05	149	5.8	5.5	75	15	1.4±0.05	137	6.0
Sep	165	16	1.0±0.02	237	3.2	3.3	45	14	1.7±0.02	55	4.8
Oct	90	20	1.8±0.02	344	3.1	3.1	48	15	1.4±0.03	67	2.8
Nov-Dec	31	10	1.4±0.05	93	2.5	2.1	5	4	0.8±0.03	12	1.8

Numerical and gravimetric percentages of the main food categories are shown in Fig. 10.4. After feeding exclusively on calanoid copepods both species shifted to fish, mysids and amphipods at about 50 mm SL. From about 100 mm SL both species fed nearly exclusively on shrimp and small fish.

According to Jones' model, bib consumed 0.29 g ADW m^{-2} yr^{-1}, whiting 0.18 g ADW m^{-2} yr^{-1}. Daily feeding coefficient φ was between 4 and 6 % of body weight in summer and declined to 2 to 3 % in autumn. For bib there is little difference between φ as estimated through Pennington's procedure and the more classical approach using the average stomach content (Table 10.2).

The P:C ratio was 0.45 for bib and 0.36 for whiting. Using the P:C ratio of 0.34 (Pihl 1982) total consumption amounted to 0.38 g ADW m^{-2} yr^{1} for bib and to 0.19 g ADW m^{-2} yr^{1} for whiting. A major part of this consumption consisted of a restricted number of species (Fig. 10.5), mainly the brown shrimp *Crangon crangon*, two species of goby *Pomatoschistus minutus* and *P. lozanoi* and larval and early postlarval herring *Clupea harengus* and sprat *Sprattus sprattus*. In bib, which has a more diverse diet (Shannon-Wiener H' = 1.05) than whiting (H' = 0.61), other fishes such as young sandeel *Ammodytes tobianus*, dragonet *Callionymus lyra*, early postlarval flatfish and gadoids occurred on a par with juvenile clupeids. The only other important prey were three mysids *Gastrosaccus spinifer*, *Schistomysis kervillei* and *S. spiritus* and two amphipods *Gammarus crinicornis* and *Atylus swammerdami*.

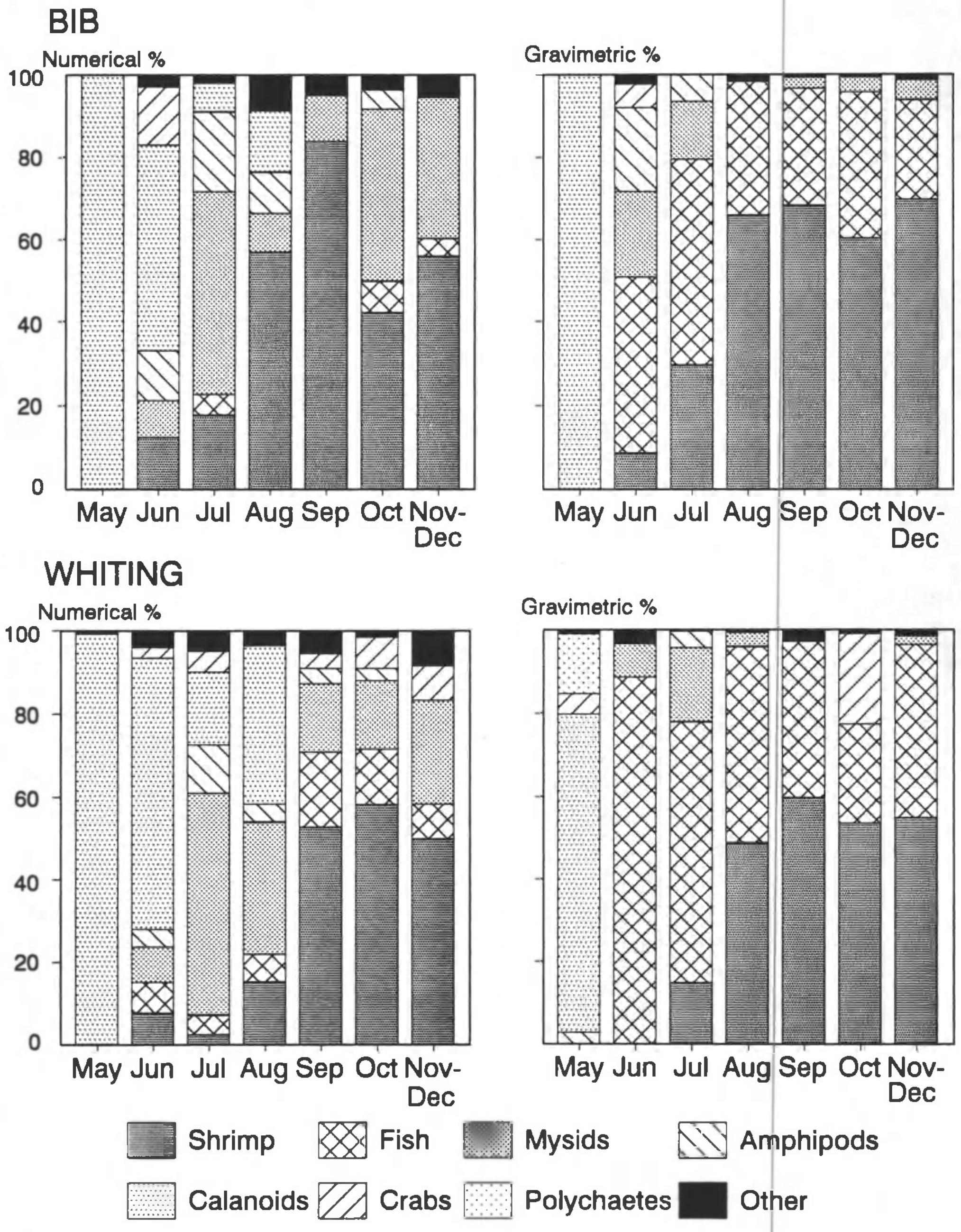


Fig. 10.4. Numerical and gravimetric food composition for bib and whiting.

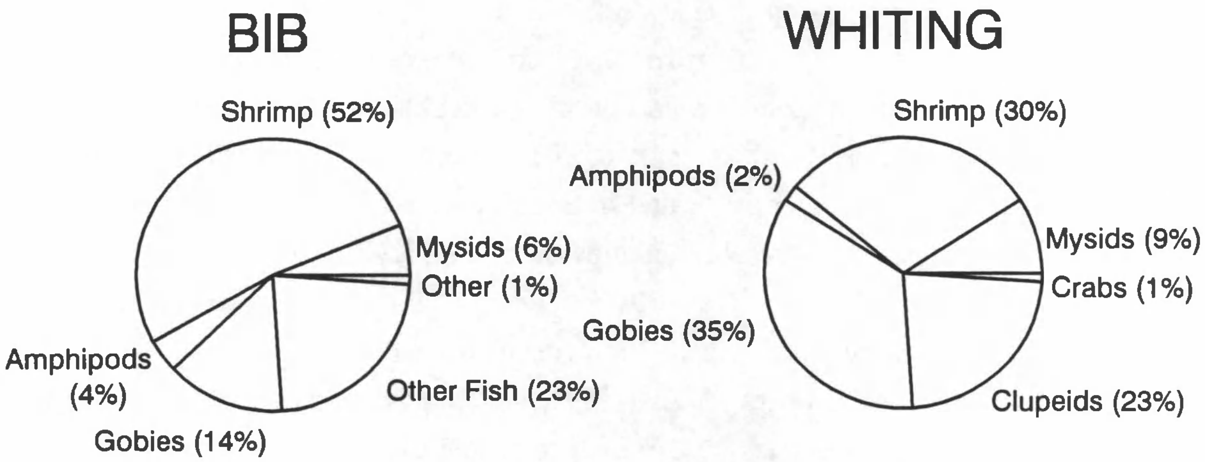


Fig. 10.5. Partitioning of food consumption by 0-group bib and whiting (June through December) for the main prey categories.

DISCUSSION

The estimates of all the variables in this paper are subject to various sources of bias. Most of these have been discussed by Patterson (1985) but in the present study the estimate of net efficiency, defined as the percentage of 0-group gadoids, feeding on or above the sampled surface area, caught in the net, is an added major source of uncertainty. The assumption that net efficiency is only 20 % is something of a wild guess. Following Kuipers (1975) there are four possible ways for fish in the trawl path to escape from an approaching beam trawl: through the meshes, underneath the ground rope, over the beam and sideways. Escapement through the meshes can be assumed to be low once the fish have reached a certain size, i.e. from July onwards. Creutzberg *et al.* (1987), though they state that pelagic fish such as whiting are not supposed to be influenced by the number of tickler chains on a beam trawl, found that the slope relating numbers caught on sandy bottoms to the number of tickler chains used was actually significantly different from zero in whiting. Variability in whiting catches was high but using three tickler chains Creutzberg *et al.* (1987) caught 1.5 times more whiting than with 1 tickler chain. Catches reached a plateau at three tickler chains. Therefore there seems to be some escapement under the gear when using only one tickler chain on sandy bottoms. Engås & Godø (1989) also report on substantial numbers of small gadoids escaping under an, admittedly quite different, trawled gear. The observations of Creutzberg *et al.* (1987) put maximum efficiency at 68 %. Bib and whiting are fast swimmers, so an unknown proportion of, especially the larger fish, can be expected to be able to avoid the gear by moving up or sideways. Moreover, as bib and whiting are pelagic at first and, even when becoming demersal, do not spend all of their time in close proximity to the bottom, some proportion of the population is also out of reach of the gear, the headrope of which is at 0.55 m from the bottom. Net efficiency is therefore unlikely to be over 50 % and in this study it was assumed to be a lot less. This means there are considerable margins of uncertainty to the estimates based on this assumption. If efficiency were 40 % density, biomass and production would only be half of the estimates given. More detailed studies on net efficiency, along the lines proposed by Kuipers *et al.* (1992), are clearly warranted. Only then can studies of fish trophodynamics be expected to match the accurracy of macrobenthic studies.

Growth as recorded in this study closely matches the results from other studies: in Moroccan waters (Coupé & Maurin 1955) and on the Atlantic coast of Spain (Oliver 1949) 0-group bib averaged between 125 and 130 mm SL by the end of the first growth season. By February of the next year the modal class reaches 150 mm SL in the southern North Sea (Desmarchelier 1985a). Fish collected from the intake screens of power stations have a seemingly slower growth: modal length class of bib in the Severn estuary increased from 40-49 mm SL in August to 70-79 mm SL in November-December (Claridge & Potter 1984). Similarly 0-group whiting in the Severn estuary grew from 60-70 mm SL in June-July to only 100 mm SL in December (Henderson & Holmes 1989). This slow 'growth' is probably an artefact of the collection method. Perhaps the larger 0-group gadoids have sufficiently high swimming speeds to avoid being sucked into the power station. On the Scottish West Coast whiting grew from about 100 mm SL in July to about 160 mm SL in November (recalculated from Gordon 1977a). This is very similar to growth in Kiel Bight (Arntz & Weber 1972) and closely resembles the results of the present study.

As in other studies fish 'growth' as defined here is a combination of true growth of individuals, predation (possibly size-selective), migration (probably also dependent on size) and mesh selection in an unknown mixture. Mean lengths in November and December are less reliable because of the low numbers of 0-group caught. The apparent length decrease of bib in December may be caused by differential migration, the largest fish leaving the area first. The same phenomenon was observed in other gadoids (Cooper 1980).

As can be judged from the standard errors of the densities (Table 10.1) the spatial distribution of both species is very patchy. The concentration in the ebb tidal delta of the Grevelingen, which is especially strong in the early part of the year and is most pronounced in bib, may be partly caused by passive transport into the area. The current patterns in the ebb tidal delta of the Grevelingen create a sink for mud and detritus. Other neutrally buoyant particles e.g. macrobenthos larvae, larval decapods and fish eggs and larvae may also be trapped in the area (Hamerlynck *et al.* 1992). According to Cooper (1980) 0-group gadoids in Scottish waters reach their nurseries mostly through active migration. Just like postlarval flatfish (Rijnsdorp *et al.* 1985) juvenile gadoids are probably rather versatile. They can make use of the residual current for passive drift but, through vertical migration, they may also be able to make use of the tidal currents to move in the opposite direction.

The observed shift in bib distribution from the ebb tidal delta of the Grevelingen to the ebb tidal delta of the Oosterschelde may be partly due to migration, but there may be an add-on effect of 0-group bib leaving the Oosterschelde proper. This second effect may also form the basis of the slight increase in density of bib in September and of whiting in October (Table 10.1).

The estimates of the instantaneous mortality rate are a combination of natural mortality, (indirect) fishing mortality and migration. Indirect fishing mortality of 0-group gadoids in the area is thought to be low since few shrimp trawlers operate in this part of the Voordelta. Migration can be an important contributing factor as it is well known that 0-group bib and whiting migrate to deeper areas by the end of their first growth season. Migration is thought to be the main cause for the sudden decrease in whiting densities after October. Therefore the last two months were not used for the calculation of Z in this species.

The Production:Biomass (P:B) ratio calculated is higher than the often used P:B = 2.75 (Elliott & Taylor 1989) or 2.5 (Hostens & Hamerlynck in press). These last two figures may be valid for mixed age groups of fishes but less so for the 0-group.

For whiting there is close similarity between consumption estimated directly from the stomach contents and indirectly from production using a Production:Consumption (P:C) ratio of 0.34. For bib the estimate using Jones' model is about 25 % lower than using the P:C ratio. Possibly Jones' model has limited applicability for the deeper bodied and shorter lived *Trisopterus* species. The feeding coefficient φ is in close agreement to the findings of Daan (1973) who gives 5.3 % for North Sea cod of 100 mm (probably total length, measurement procedure not mentioned in Daan 1973) and 2.5 % for cod of 200 mm.

Food preference at different sizes closely resembles the pattern observed by other authors (see references in the introduction): first calanoids, then mysids and amphipods and finally shrimp and small fishes.

Our estimate of the P:C ratio, or ecological efficiency, seems high for bib, but for whiting it is closely similar to Pihl's (1982) estimate for 1-group cod and to the estimate of Jones & Hislop (1978) for different gadoid species. All these estimates are much higher than the 0.11 to 0.18 suggested for whiting by Patterson (1985), though his data did not include 0-group fish. Moreover if consumption was calculated by Patterson (1985) using the stated formula, it may have been seriously overestimated, leading to a very low P:C.

Though Pennington (1985) showed that one should first raise the individual weights in the stomachs to a certain power (0.43 in the case of Jones' model) and then calculate the mean to find an unbiased estimator of food consumption, this procedure was not followed in the present study, nor by Hislop *et al.* (1991). The possible consequences of this are illustrated in a very extreme example given in Ursin *et al.* (1985) where consumption was overestimated by over 40 % using our procedure. However, as long as variability in the amount of food in the stomachs of the fish is low, which, in the present study, is the case for both species, the final result of both procedures is rather similar and the calculations are very substantially simplified using the average of stomach content per sample as the input to Jones' model. Thus in bib, there was on average less than 0.4 % difference between % body weight consumption using Pennington's procedure and the simpler approach. From the variability in stomach contents in whiting it seems highly likely that, if any, the difference between the two procedures for whiting would have been of the same order of magnitude. However, Pennington's procedure should be used in species taking single meals of large and heavy items with long (e.g. several days) non-feeding intervals between two meals.

ACKNOWLEDGEMENTS

The second author acknowledges a grant from the IWONL. The research was partly subsidised by the Dutch Rijkswaterstaat, dienst Getijdewateren Middelburg and the Belgian FKFO project 32.0086.88. Sampling was greatly facilitated by the seamanship and help of W. Röber, C. van Sprundel, P. de Koeyer, H.W. Francke and G. Desmet.

Contribution no. 587 of the Centre for Estuarine and Coastal Ecology, Yerseke.

IMPLICATIONS

For ecology to be taken seriously as a science it has to distinguish itself from natural history. In order to do so, ecology must demonstrate that it is capable of predicting what will happen in natural systems under specific scenarios. To achieve this predictive capacity, knowledge on the ecosystem has to be formalised into models. These models can then be used both for understanding and for management of ecosystems. For the models to have predictive power they need to be simple, otherwise the total system error will be swamped by the measurement error associated to every input parameter (Sugihara *et al.* 1986). Most marine systems are highly complex with a great many species having a wide range of different life histories and occurring in a highly dynamic environment. Evidently, details on the various properties of all the elements in the system can not be incorporated into the model and therefore some lumping seems unavoidable.

Taxonomic lumping, i.e. aggregating related species into broader categories, is one of the easiest strategies: one can afford to spend less time (and therefore money) identifying individual species and, e.g. in the coastal area of Chapter 2, one might suffise with broad categories such as herring-like, cod-like, flatfish-like and goby-like, or simply fish. For an extreme example, namely lumping to phylum level (within the macrobenthos), see Warwick & Clarke (1993).

For this lumping to be successful it is hoped that the crucial rates in taxonomically similar species are the same, i.e. that they grow and die at the same rate. For this to be the case they will probably need to have similar prey and similar predators. This hope runs counter the notion of the competitive exclusion principle (Hardin 1960) which states that a number of species N cannot coexist on less than N resources. The implication is that the more similar two species are the more likely they are to partition resources in important dimensions of resource utilisation hyperspace (MacArthur 1970) and especially in the dimensions of food, time and habitat. If two very similar species eat completely different prey types (perhaps even at different trophic levels), if they make use of the environment at exactly opposite times (day-night or different seasons) and if they actually belong to different communities (i.e. occur in dissimilar microhabitats where they are subject to different predators and competitors), lumping them may not be very adequate. Though many species pairs have been the subject of ecological studies, an opportunity such as presented by *Pomatoschistus minutus* and *Pomatoschistus lozanoi* is attractive. The species are extremely similar (Chapter 3) and it was only through the patient detective work by Mark Fonds (Fonds 1973) that the existence of two separate species was documented. Fonds first noted different modes in the size-frequency distribution, then went on to do vertebral counts, noted differences in pigmentation, then found differences in the papillae on the head. He then cultured these differently pigmented gobies and found vertebral number to be genetically determined, etc. The documentation of this endeavour is well worth reading (Fonds 1973). It is amazing to find that such abundant North Sea vertebrates have been recognised as being composed of separate species as late as 1973. So an interesting question is, can we lump *P. minutus* and *P. lozanoi* into a single sand goby group? Most of the chapters in the present thesis would tend towards a no: there is a clear difference in habitat use as both species are indicator species for different communities of epibenthic invertebrates and demersal fishes (Chapter 2). Though most of the parasite species recorded are common to both species (Chapter 4), there are clear differences in both prevalence and mean intensity of infection. *P. minutus* and *P. lozanoi* spawn at different times of the year (Chapter 8) and similar sized gobies of both species use food resources quite differently throughout most of the year (Chapters 5 and 8). Incidently, Fonds (1973) estimated the parameters of the von Bertalanffy growth equation for the lumped species and found K values of around 0.9 for an L_∞ of about 90 mm (Total length). Preliminary calculations with data from the Voordelta suggest a K of 1.2 to 1.4 for the species taken separately, while a K of about 0.8 was found for the lumped species. The L_∞ of *P. minutus* was about 80 mm (Standard length) and for *P. lozanoi* about 65 mm (Arellano & Hamerlynck unpubl. data). If gobies were of commercial importance and if a yield calculation would have been performed on the basis of the lumped growth data, it would be quite far off the mark. The importance of the study of daily growth rings for an accurrate assessment of the growth rate, independent of mesh size selection (see also Chapter 10) can not be overemphasised. Naturally, if gobies are predator-controlled, as is expected (Chapters 1 and 10), and if their predators roam widely enough to cover the possibly subtly partitioned microhabitats of both gobies, and if it doens't make a blind bit of difference to the predator if he chews on a *P. minutus* or on a *P. lozanoi*, then all the delicate lower trophic level differences may be simply obliterated from the seafloor.

For studies of energy flow, the two goby congenerics under consideration are a bit of a nightmare. For example, Doornbos & Twisk (1987) estimated that more than 90 % of the production by gobies in Lake Grevelingen occurred before the fish had reached a mean length at which they became fully catchable with fine meshed nets. The strong fluctuation in feeding intensity recorded over 24 hours (Chapter 6) and its high spatial variability (Chapter 9) make any estimate of daily ration from stomach content data rather fancyful. Though theoretically predator-limited, the suspected difference in feeding intensity over a spring-neap cycle (Chapter 6) and its impact on growth, as exemplified by the banding pattern in the otoliths, may be an indication of, at least occasional, food limitation. This implies that food conversion factors established in the laboratory are needed to be able to use growth and mortality data to estimate food consumption over longer time intervals (see also Chapter 10).

A further point worth investigating is an assessment of the differences between the realised niches and the fundamental niches of the species (Hutchinson 1958). This question relates to the distinction between present day competition, be it of the exploitative or of the interference type, and the ghost of competition past (Connell 1980). If the species show high plasticity in their resource use they can replace one another in the food web when competitive release occurs. If one of the species has a failed breeding season (for example because a few containers of Uraniumhexafluoride have exploded on the sea floor during its spawning peak) the other species will take over the empty resource space and total output from the lumped two species will be indistinguishable from a 'normal' say 50%-50% abundance. If, on the other hand, we are only observing the ghost of competition past, then the character displacement that has occurred as an adaptation to the more restricted niche will potentially preclude any simple replacement of one species by the other.

As a consequence, before lumping similar species, an assessment of some of these critical aspects may be interesting. This is not to say that before models can be built everything on every species occurring on planet earth should be known. On the contrary, when masses of data are available one has to be extremely selective as to what will actually be put into the model. For example, the 'simple' multispecies fishery model of the North Sea proposed by Andersen & Ursin (1977), which only considers the ten dominant commercial species, needs more than 800 input parameters. Though conceptually interesting, the model is completely intractable and its predictive power is zero. A good model leaves out as much as possible. It is not because the data are there, that they should be incorporated into the model. Still this 'inclusive' strategy was recently defended by a group of modellers (Brinkmann *et al.* 1993).

According to Ernest Rutherford, all scientific activity outside the domain of fundamental physics is an elaborate form of stamp collecting. So be it. Reliable data on a large number of species, from a wide range of different ecosystems, seem to be a prerequisite for the establishment of more general and more fundamental relationships that may eventually considerably simplify the modellers' predicament. On the other hand, painstakingly collecting all these little facts does not automatically lead to the construction of a major scientific edifice, such as a theory. Thinking hard and experimenting must also contribute. Physicists should not forget that, at least for some of their early successes in theory formation, they could fall back on scores of years of accurrate recordings of the movements of the planets. Understanding of physical systems that are not deterministic in nature came quite a bit later. In ecology, typically dealing with a lot of stochasticity, long-term data sets are still very few and scanty (Likens 1989).

As stated before, most of the crucial rates modellers of ecosystems are interested in (such as growth and mortality), are exponential rates. We are therefore dealing with non-linear dynamical systems. When aggregating exponential rates into a function that is to be an acceptable representative of the constituent rates, it is advisable for the constituent rates to be similar (the Lange-Hicks condition) (Sugihara *et al.* 1986). A logical consequence is then to aggregate according to size or age-class, as many of the important rates, such as respiration and mortality, will be related to size rather than to taxonomic closeness. For example, the predators and prey (and the rates at which these consume and are consumed) of a 50 cm cod will presumably be more similar to those of a 50 cm haddock than to those of a 5 cm cod. An interesting size-structured model of the lower trophic levels of a tropical neritic system was presented by Roff *et al.* (1990). In some areas at least, like the brackish part of the Westerschelde, it may be possible to build a size-structured model of the higher trophic levels. Only a few species are dominant in the system and the food supply is such that in spring mysids, small shrimp and early postlarval fishes will all eat the copepod *Eurytemora*. When the predators have reached a certain size threshold, they will switch to *Neomysis integer* with a sprinkling of *Gammarus salinus*. The ones that grow beyond that size then switch to *Crangon crangon* and *Pomatoschistus whateveri*. Next, the big ones conveniently move out to sea. There are therefore only a few boxes to fill, not with similar species in a box, but with similar size classes of both vertebrates and invertebrates in each box. As in the estuary the food chain is dominated by the detrital input from the river (Hamerlynck *et al.* submitted b) perhaps this would be tractable. Alternatively one may say that in estuarine ecosystems, in terms of grams carbon per m^2 per year, only the micro-organisms play a significant role and one can leave the higher trophic levels to fend for themselves.

In the coastal zone a higher trophic level model would presumably have to include both size and trophic guilds, i.e. mesozooplankton feeders of between 20 and 55 mm, mesozooplankton feeders of between 55 and 100 mm, macrobenthos feeders of the same size groups, hyperbenthos feeders, etc.

PREDICTIVE EPILOGUE

As ecologists have to predict to be taken seriously, I predict that *Gobiusculus flavescens* is a likely candidate to take over the niche vacated by *Pomatoschistus lozanoi* in the Oosterschelde. The hypothesis is that before the storm surge barrier was built *P. lozanoi* was well established in the system, just like it is in the Westerschelde and the Voordelta. There is some circumstantial evidence in the form of an autumn sample of 100 gobies collected in the Oosterschelde by Gerdinus Doornbos in the early 1980's. The sample spent a long time in a deepfreezer and was put into alcohol after thawing. This procedure did not make the identification easier but, tentatively, the sample contained about 70 % *P. lozanoi* (a qualifier for the Journal of Irreproducible Results, if ever there was one). In the post-barrier situation *P. lozanoi* hardly ever represents more than 5% of Oosterschelde gobies in the marine part, and less than 2% in the inner part (Chapter 2). The obvious explanation would then be that, with the increased water transparency (Bakker *et al.* 1990), visual predators (especially 0-group gadoids) have increased, not only in abundance (Hamerlynck & Hostens in press, Hostens & Hamerlynck in press) but also in efficiency. In August, when the young gadoids have reached about 100 mm SL, gobies become an important food item for them (Chapter 10). This coincides with the first catches of very high numbers of *P. lozanoi* in the Voordelta and the Westerschelde. Therefore, *P. lozanoi* are probably also migrating massively into the Oosterschelde. There they are probably very efficiently wiped out by gadoids and other visual predators, including *P. minutus*. In contrast to its congener, *P. minutus* spawns in the Oosterschelde and does so a few months earlier. By the time of the abundance peak of gobyfeasting gadoids, a large part of the *P. minutus* population has already outgrown gadoid gape size. To come back to *Gobiusculus flavescens*, this is a zooplanktivorous goby living among macro-algae in fjords (Fosså 1991). In some aspects the Oosterschelde now resembles a fjord (including the sill at the entrance). With increasing water temperatures, macro-algae in the Oosterschelde will be less susceptible to destruction by ice-floes. With time a few *Gobiusculi*, and hopefully also some *Gobiuscula*, may enter the Oosterschelde and find shelter from the gadoids among the algae. The *G. flavescens* population will then feed on the autumn zooplankton bloom that used to sustain *P. lozanoi*. Because of the piscivores, densities of *G. flavescens* will remain low and *Gobiusculus* will mostly be confined to the hard substrates in proximity to fucoids. The model however does not predict when this will happen, but I guess 100 years would be a reasonable time scale.

REFERENCES

Aarnio, K. & Bonsdorff, E. 1993. Seasonal variation in abundance and diet of the sand goby *Pomatoschistus minutus* (Pallas) in a northern Baltic archipelago. Ophelia 37: 19-30.

Aarnio, K., Sandberg, E. & Bonsdorff, E. 1991. Benthic predation on shallow-water macro- and meiofauna in the Baltic Sea: an experimental comparison between *Pomatoschistus minutus* and *Saduria entomon*. Annales Zoologici Fennici 28: 41-48.

Aerts, P. 1992. Fish biomechanics: purpose or means? Netherlands Journal of Zoology 42: 430-444.

Andersen, N.G. 1984. Depletion rates of gastrointestinal content in common goby (*Pomatoschistus microps* (Kr.)). Effects of temperature and fish size. Dana 3: 31-42.

Andersen, K.P. & Ursin, E. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Meddelelser fra Danmarks Fiskeri- og Havundersøgelser, New Series 7: 319-435.

Ansell, A.D. & Gibson, R.N. 1990. Patterns of feeding and movement of juvenile flatfishes on an open sandy beach. In: Barnes, M. & Gibson, R.N., (Eds). Trophic relationships in the marine environment. Proceedings of the 24th European Marine Biology Symposium. Aberdeen University Press, Aberdeen: 191-207.

Antholz, B., Meyer-Antholz, W. & Zander, C.D. 1991. Feeding activities of two euryhaline small-sized fish in a western Baltic brackish fjord. Helgoländer Meeresuntersuchungen 45: 287-300.

Armstrong, M.J. 1982. The predator-prey relationships of Irish Sea poor-cod (*Trisopterus minutus* L.), pouting (*Trisopterus luscus* L.), and cod (*Gadus morhua* L.). Journal du Conseil international pour l'Exploration de la Mer 40: 135-152.

Arntz, W.E. 1974. Die Nahrung juveniler Dorsche (*Gadus morhua* L.) in Kiel Bay. Berichte der deutschen wissenschaftlichen Kommissionen für Meeresforschung 23: 97-120.

Arntz, W.E. & Weber, W. 1972. Zur Herkunft des Wittlings (*Merlangius merlangus* [L.]) der Kieler Bucht. Berichte der deutschen wissenschaftlichen Kommissionen für Meeresforschung, 22: 385-397.

Arthur, W. 1987. The niche in competition and evolution. Wiley, Chichester. 175 pp.

Assis, C.A., Almeida, P.R., Moreira, F., Costa, J.L. & Costa, M.J. 1992. Diet of the twaite shad *Alosa fallax* (Lacépède) (Clupeidae) in the river Tagus estuary, Portugal. Journal of Fish Biology 41: 1049-1050.

Bakker, C., Herman, P.M.J. & Vink, M. 1990. Changes in seasonal succession of phytoplankton induced by the storm surge barrier in the Oosterschelde (S.W. Netherlands). Journal of Plankton Research 12: 947-972.

Barel, C.D.N. 1983. Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). Netherlands Journal of Zoology 33: 357-424.

Benvegnú, G. 1971. Datos biométricos y biológicos sobre la faneca [*Trisopterus luscus* (L., 1758)] (Gadidae) del Cantábrico. Boletin del Instituto Español de Oceanografia 148: 1-42.

Berg, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). Marine Biology 50: 263-273.

Berge, J.A., Johannessen, K.I. & Reiersen, L.-O. 1983. Effects of the water soluble fraction of North Sea crude oil on the swimming activity of the sand goby, *Pomatoschistus minutus* (Pallas). Journal of Experimental Marine Biology and Ecology 68: 159-167.

Besten, P.J. den 1991. Effects of cadmium and PCBs on reproduction of the sea star *Asterias rubens*. Unpubl. thesis, Rijksuniversiteit Utrecht.

Blaber, S.J.M. & Blaber, T.G. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17: 143-162.

Boddeke, R., Driessen, G., Doesburg, W. & Ramaekers, G. 1986. Food availability and predator presence in a coastal nursery area of the brown shrimp (*Crangon crangon*). Ophelia 26: 77-90.

Boisclair, D. & Leggett, W.C. 1988. An in situ experimental evaluation of the Elliott and Persson and the Eggers model for estimating fish daily ration. Canadian Journal of Fisheries and Aquatic Sciences 45: 138-145.

Boujard, T. & Leatherland, J.F. 1992. Circadian rhythms and feeding time in fishes. Environmental Biology of Fishes 35: 109-131.

Braak, C.J.F. ter 1988. CANOCO - a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Agricultural Mathematics Group, Ministry of Agriculture and Fisheries. 77 pp.

Braak, C.J.F. ter & Prentice, I.C. 1988. A theory of gradient analysis. Advances in Ecological Research 18: 271-315.

Braber, L. & Groot, S.J. de 1973. The food of five flatfish species (Pleuronectiformes) in the southern North Sea. Netherlands Journal of Sea Research 6: 163-172.

Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27: 325-349.

Brinkmann, A., Raaphorst, W.van & Malmgren-Hansen, A. 1993. Ecological modelling in WASP. Oral presentation at the MAST days and EUROMAR Market. Commission of the European Communities DG XII. March 7-12 1993, Brussels.

Broek, W.L.F van den 1978. Dietary habits of fish populations in the lower Medway estuary. Journal of Fish Biology 13: 645-654.

Caine, E.A. 1991. Caprellid amphipods: fast food for the reproductively active. Journal of Experimental Marine Biology and Ecology 148: 27-33.

Cattrijsse, A. 1987. Modula-2 programma voor data-verwerking in visserijbiologie. M.Sc. thesis, Free University of Brussels (in Dutch).

Cattrijsse, A., Mees, J. & Hamerlynck, O. (in press). The hyperbenthic amphipoda and isopoda of the Voordelta and the Westerschelde estuary. Cahiers de Biologie Marine.

Claridge, P.N. & Potter, I.C. 1984. Abundance, movements and size of gadoids (Teleostei) in the Severn Estuary. Journal of the marine biological Association of the United Kingdom 64: 771-790.

Claridge, P.N., Hardisty, M.W., Potter, I.C. & Williams, C.V. 1985. Abundance, life history and ligulosis in the gobies (Teleostei) of the inner Severn Estuary. Journal of the marine biological Association of the United Kingdom 65: 951-968.

Claridge, P.N., Potter, I.C. & Hardisty, M.W. 1986. Seasonal changes in movements, abundance, size composition and diversity of the fish fauna of the Severn Estuary. Journal of the marine biological Association of the United Kingdom 66: 229-258.

Clarke, K.R. & Green, R.H. 1988. Statistical design for a 'biological effects' study. Marine Ecology - Progress Series 46: 213-226.

Cochran, P.A. 1979. Comments on some recent methods for estimating food consumption by fish. Journal of the Fisheries Research Board of Canada 36: 1018.

Cole, K.S. 1982. Male reproductive behaviour and spawning success in a temperate zone goby, *Coryphopterus nicholsi*. Canadian Journal of Zoology 60: 2309-2316.

Colwell, R.K. & Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 55: 131-138.

Cooper, A. 1980. Gadoid populations of western Scottish sea lochs and their exchanges with west coast stocks. In: Freeland, H.J., Farmer, D.M. & Levings, C.D. (Eds.). Fjord oceanography. Plenum Press, New York: 415-421.

Costa, M.J. 1986. Les poissons de l'estuaire du Tage. Cybium 10: 57-75.

Costa, M.J. 1988. Écologie alimentaire des poissons de l'estuaire du Tage. Cybium 12: 301-320.

Costa, M.J. & Elliott, M. 1991. Fish usage and feeding in two industrialised estuaries - the Tagus, Portugal, and the Forth, Scotland. In: Elliott, M. & Ducrotoy, J.P. (Eds.). Estuaries and coasts: spatial and temporal intercomparisons. Olsen & Olsen, Fredensborg: 289-297.

Costa, J.L., Assis, C.A., Almeida, P.R., Moreira, F.M. & Costa, M.J. 1992. On the food of the European eel, *Anguilla anguilla* (L.) in the upper zone of the Tagus estuary, Portugal. Journal of Fish Biology 41: 841-850.

Coupé, R. & Maurin, C. 1955. Note préliminaire sur la croissance de *Gadus luscus* Cuv. Val. au Maroc. Annales Biologiques 12: 125-127.

Craeymeersch, J.A., Hamerlynck, O., Hostens, K., Vanreusel, A. & Vincx, M. 1990. De ekologische ontwikkeling van de Voordelta. Deelrapport 1. De huidige ekologische situatie. Internal Report Delta Institute of Hydrobiological Research and University of Gent. 92 pp (in Dutch).

Creech, S. 1991. An electrophoretic investigation of populations of *Atherina boyeri* Risso, 1810 and *A. presbyter* Cuvier, 1829 (Teleostei: Atherinidae): genetic evidence in support of the two species. Journal of Fish Biology 39: 807-816.

Creutzberg, F. 1985. 'Aurelia'-cruise reports of the benthic fauna of the southern North sea. Introductory report. Interne Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel 1979-4: 1-31.

Creutzberg, F. & Witte, J.IJ. 1989. An attempt to estimate the predatory pressure exerted by the lesser weever, *Trachinus vipera* Cuvier, in the southern North Sea. Journal of Fish Biology 34: 429-449.

Creutzberg, F., Duineveld, G.C.A. & Noort, G.J. van 1987. The effects of different numbers of tickler chains on beam-trawl catches. Journal du Conseil International pour l'Exploration de la Mer 43: 159-168.

Crisp, D.J. 1984. Energy flow measurements. In: Holme, N.A. & McIntyre, A.D. (Eds.). I.B.P. Handbook no. 16: Methods for the study of marine benthos. Blackwell, Oxford: 284-372.

Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Netherlands Journal for Sea Research 6: 479-517.

Daan, N., Bromley, P.J, Hislop, J.R.G. & Nielsen, N.A. 1990. Ecology of North Sea fish. Netherlands Journal of Sea Research 26: 343-386.

Damme, P.A. van, Hamerlynck, O. & Ollevier, F. (in prep.) Population dynamics of *Lernaeocera lusci* (Basset-Smith) in the Voordelta.

Daro, M.H. & Gijsegem, B. van 1984. Ecological factors affecting weight, feeding, and production of five dominant copepods in the Southern Bight of the North Sea. Rapports et Procès-verbaux du Conseil international pour l'Exploration de la Mer 183: 226-233.

Desmarchelier, M. 1985a. Croissance et reproduction du tacaud (*Trisopterus luscus* L. 1758) en Manche est et sud de la Mer du Nord. International Council for the Exploration of the Sea CM 1985/G: 29.

Desmarchelier, M. 1985b. La pêche du tacaud (*Trisopterus luscus*) en Manche et dans le sud de la Mer du Nord - aperçus statistiques et économiques. International Council for the Exploration of the Sea CM 1985/G: 43.

Dijke, B. van & Buijs, J. 1987. Dataverwerking project Voordelta. Rijkswaterstaat Dienst Getijdewateren. Notitie GWAO 87.505: 58 pp. (in Dutch).

Doornbos, G. 1984. Piscivorous birds on the saline Lake Grevelingen, the Netherlands: Abundance, prey selection and annual food consumption. Netherlands Journal of Sea Research 18: 457-479.

Doornbos, G. & Twisk, F. 1987. Density, growth and annual food consumption of gobiid fish in the saline Lake Grevelingen, the Netherlands. Netherlands Journal of Sea Research 21: 45-74.

Duursma, E.K., Merks, A.G.A. & Nieuwenhuize, J. 1988. Exchange processes in estuaries such as the Westerschelde, an overview. Hydrobiological Bulletin 22: 7-20.

Eck, G.T.M. van, Pauw, N. de, Langenbergh, M. van den & Verreet, G. 1991. Emissies, gehalten, gedrag en effecten van (micro)verontreinigingen in het stroomgebied van de Schelde en het Schelde-estuarium. Water 60: 164-181. (in Dutch).

Eggers, D.M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. Journal of the Fisheries Research Board of Canada 34: 290-294.

Eggers, D.M. 1979. Comments on some recent methods for estimating food consumption by fish. Journal of the Fisheries Research Board of Canada 36: 1018-1019.

Elliott, J.M. 1979. Comments on some recent methods for estimating food consumption by fish. Journal of the Fisheries Research Board of Canada 36: 1020.

Elliott, J.M. & Persson, L. 1978. The estimation of daily rates of food consumption for fish. Journal of Animal Ecology 47: 977-991.

Elliott, M. & Taylor, C.J.L. 1989. The structure and functioning of an estuarine/marine fish community in the Forth estuary, Scotland. Proceedings of the 21st European Marine Biology Symposium, Gdansk: 227-240.

Elliott, M., O'Reilly, M.G. & Taylor, C.J.L. 1990. The Forth estuary: a nursery and overwintering area for North Sea fishes. Hydrobiologia 195: 89-103.

Engås,A. & Godø, O.R. 1989. Escape of fish onder the fishing line of a Norwegian sampling trawl and its influence on survey results. Journal du Conseil International pour l'Exploration de la Mer 45: 269-276.

Essink, K. 1989. Chemical monitoring in the Dutch Wadden Sea by means of benthic invertebrates and fish. Helgoländer Meeresuntersuchungen 43: 435-446.

Evans, S. 1983. Production, predation and food niche segregation in a marine shallow soft-bottom community. Marine Ecology - Progress Series 10: 147-157.

Evans, S. 1984. Energy budgets and predation impact of dominant epibenthic carnivores on a shallow soft bottom community at the Swedish west coast. Estuarine, Coastal and Shelf Science 18: 651-672.

Evans, S. & Tallmark, B. 1979. A modified drop-net method for sampling mobile epifauna on marine shallow sandy bottoms. Holarctic Ecology 2: 58-64.

Feinsinger, P., Spears, E.E. & Poole, R.W. 1981. A simple measure of niche breadth. Ecology 62: 27-32.

Fernandez, L., Freire, J. & Gonzalez-Gurriaran, E. (in press). Diel feeding activity of demersal fish in the Ria de Arousa (Galicia, NW Spain). Journal of Fish Biology.

Field, J.G., Clarke, K.R. & Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology- Progress Series 8: 37-52.

Fitzhugh, G.R. & Fleeger, J.W. 1985. Goby (Pisces: Gobiidae) interactions with meiofauna and small macrofauna. Bulletin of Marine Science 36: 436-444.

Fonds, M. 1973. Sand gobies of the Dutch Wadden Sea (*Pomatoschistus*, Gobiidae, Pisces). Netherlands Journal of Sea Research 6: 417-478.

Fonds, M. 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. In : Naylor, E. & Hartnoll, R.G.(Eds.). Cyclic phenomena in marine plants and animals. Proceedings of the 13th European Marine Biology Symposium. Pergamon Press, Oxford: 151-156.

Fosså, J.H. 1991. The ecology of the two-spot goby (*Gobiusculus flavescens* Fabricius): the potential for cod enhancement. ICES marine Science Symposia 192: 147-155.

Froese, R. 1988. The use of quadratic discrimination functions in connection with video-based measurements for identification of fish larvae. International Council for the Exploration of the Sea CM 1988/L: 11 (mimeo).

Fry, J.C. 1993. Biological data analysis, a practical approach. Oxford University Press, Oxford. 418 pp.

Gee, J.M. 1987. Impact of epibenthic predation on estuarine intertidal harpacticoid copepod populations. Marine Biology 96: 497-510.

Gee, J.M. 1989. An ecological and economic review of meiofauna as food for fish. Zoological Journal of the Linnean Society 96: 243-261.

Gerlach, S.A. 1977. Attraction to decaying organisms as a possible cause for patchy distribution of nematodes in a Bermuda beach. Ophelia 16: 151-165.

Gherbi-Barre, A. 1983. Biologie de *Trisopterus luscus* (L. 1758) de la baie de Douarnenez (reproduction, croissance, régime alimentaire). Unpubl. thesis, Université Bretagne Occidentale.

Gibson, R.N. 1993. Tidally-synchronised behaviour in marine fishes. In: Ali, M.A. (Ed.). Rhythms in fishes. NATO-ASI Series A. Plenum Press, New York: 67-86.

Gibson, R.N. & Ezzi, I.A. 1981. The biology of the Norway goby, *Pomatoschistus norvegicus* (Collett), on the west coast of Scotland. Journal of Fish Biology 19: 679-714.

Gibson, R.N. & Hesthagen, I.H. 1981. A comparison of the activity pattern of the sand goby *Pomatoschistus minutus* (Pallas) from areas of different tidal range. Journal of Fish Biology 18: 669-684.

Gordon, J.D.M. 1977a. The fish populations in inshore waters of the west coast of Scotland. The distribution, abundance and growth of the whiting (*Merlangius merlangus* L.). Journal of Fish Biology 10: 587-596.

Gordon, J.D.M. 1977b. The fish populations in inshore waters of the west coast of Scotland. The food and feeding of the whiting (*Merlangius merlangus* L.). Journal of Fish Biology 11: 513-529.

Haedrich, R.L. 1983. Estuarine fishes. In: Ketchum, B. (Ed.). Estuaries and enclosed seas. Elsevier, Amsterdam: 183-207.

Hamerlynck, O. 1990. The identification of *Pomatoschistus minutus* (Pallas) and *Pomatoschistus lozanoi* (de Buen) (Pisces, Gobiidae). Journal of Fish Biology 37: 723-728.

Hamerlynck, O. & Cattrijsse, A. (submitted). The food of *Pomatoschistus minutus* (Pisces, Gobiidae) in the Belgian coastal waters, and a comparison with the food of its potential competitor *P. lozanoi*.

Hamerlynck, O. & Hostens, K. 1993. Growth, feeding, production and consumption in 0-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow coastal area of the SW Netherlands. ICES Journal of marine Science 50: 81-91.

Hamerlynck, O. & Hostens, K. (in press). Changes in the fish fauna of the Oosterschelde - a ten year time series of fyke catches. Hydrobiologia.

Hamerlynck, O. & Mees, J. 1991. Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables. Oceanologica Acta vol. sp. n° 11: 205-212.

Hamerlynck, O. & Vanreusel A. (in press). *Mesacanthion diplechma* (Nematoda: Thoracostomopsidae), a link to higher trophic levels? Journal of the marine biological Association of the United Kingdom.

Hamerlynck, O., Heip, C. & Redant, F. 1986. Life history, food consumption and food resource partitioning in two sympatric gobies *Pomatoschistus minutus* and *P.*

lozanoi in the Belgian coastal waters. International Council for the Exploration of the Sea CM 1986/L.14 (mimeo).

Hamerlynck, O., Geets, A. & Damme, P. van 1989. The parasites of two sympatric gobies, *Pomatoschistus minutus* and *P. lozanoi* in the Belgian coastal waters. In: Wouters, K. & Baert, L. (Eds.). Proceedings of the Symposium 'Invertebrates of Belgium'. KBIN, Brussels: 27-30.

Hamerlynck, O., Vyver, P. van de & Janssen, C.R. 1990. The trophic position of *Pomatoschistus lozanoi* (Pisces, Gobiidae) in the Southern Bight. In: Barnes, M. & Gibson, R.N. (Eds.). Trophic relationships in the marine environment. Proceedings of the 24th European Marine Biology Symposium. Aberdeen University Press, Aberdeen: 183-190.

Hamerlynck, O., Hostens, K., Mees, J., Arellano, R.V., Cattrijsse, A., Vyver, P. van de & Craeymeersch, J.A. 1992. The ebb tidal delta of the Grevelingen: a man-made nursery for flatfish? Netherlands Journal of Sea Research 30: 191-200.

Hamerlynck, O., Hostens, K., Arellano, R.V., Mees, J. & Damme, P.A. van (in press). The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands): spatial structure. Netherlands Journal of Aquatic Ecology.

Hamerlynck, O., Cattrijsse, A. & Arellano, R.V. (submitted a). Daily ration of juvenile *Pomatoschistus lozanoi* (Pisces: Gobiidae). Influence of circadian, circatidal and semilunar rhythms.

Hamerlynck O., Mees, J., Craeymeersch, J.A., Soetaert, K., Hostens, K., Cattrijsse, A. & Damme, P.A. van (submitted b). The Westerschelde estuary: two food webs and a nutrient rich desert.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

Harmelin-Vivien, M.L., Kaim-Malka, R.A., Ledoyer, M. & Jacob-Abraham, S.S. 1989. Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. Journal of Fish Biology 34: 715-734.

Healey, M.C. 1971. The distribution and abundance of sand gobies, *Gobius minutus*, in the Ythan estuary. Journal of Zoology 163: 177-229.

Heip, C. 1989. The ecology of the estuaries of Rhine, Meuse and Scheldt in the Netherlands. In: Ross, J.D. (Ed.). Topics in Marine Biology. Scientia Marina 53: 457-463.

Heip, C., Vincx, M. & Vranken, G. 1985. The ecology of marine nematodes. Oceanography and Marine Biology Annual Review 23: 399-489.

Heip, C., Herman, P. & Soetaert, K. 1988. Data processing, evaluation and analysis. In: Higgins, R.P. & Thiel, H. (Eds.). Introduction to the study of meiofauna. The Smithsonian Institution Press, Washington: 197-231.

Heip, C., Huys, R., Vincx, M., Vanreusel, A., Smol, N., Herman, R. & Herman, P.M.J. 1990. Composition, distribution, biomass and production of North Sea meiofauna. Netherlands Journal of Sea Research 26: 333-342.

Henderson, P.A. 1989. On the structure of the inshore fish community of England and Wales. Journal of the marine biological Association of the United Kingdom 69: 145-163.

Henderson, P.A. & Holmes, R.H.A. 1989. Whiting migration in the Bristol Channel: a predator-prey relationship. Journal of Fish Biology 34: 409-416.

Herman, P.M.J., Hummel, H., Bokhorst, M. & Merks, A.G.A. 1991. The Westerschelde: interaction between eutrophication and chemical pollution. In: Elliott, M. & Ducrotoy, J.P. (Eds.). Estuaries and coasts: spatial and temporal intercomparisons. Olsen & Olsen, Fredensborg: 359-364.

Hesthagen, I.H. 1971. The winter food of the gobies from one of the deeper channels of the Belt Sea, with particular reference to the sand goby, *Pomatoschistus minutus* (Pallas). Kieler Meeresforschungen 27: 28-35.

Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427-432.

Hill, M.O. 1979. TWINSPAN - a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Ithaca. 60 pp.

Hislop, J.R.G. & MacKenzie, K. 1976. Population studies of the whiting *Merlangius merlangus* (L.) of the northern North Sea. Journal du Conseil International pour l'Exploration de la Mer 37: 98-111.

Hislop, J.R.G., Robb, A.P., Bell, M.A. & Armstrong, D.W. 1991. The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. ICES Journal of marine Science 48: 139-156.

Hofsten, A. von, Kahan, D., Katznelson, R. & Bar-El, T. 1983. Digestion of free-living nematodes fed to fish. Journal of Fish Biology 23: 419-428.

Holbrook, S.J. & Schmitt, R.J. 1989. Resource overlap, prey dynamics, and the strength of competition. Ecology 70: 1943-1953.

Horn, H.S. 1966. Measurement of "overlap" in comparative ecological studies. The American Naturalist 100: 419-424.

Hostens, K. & Hamerlynck, O. (in press). The epibenthic community of the subtidal Oosterschelde: structure, function and impact of the storm-surge barrier. Hydrobiologia.

Hummel, H., Moerland, G. & Bakker, C. 1988. The concomitant existence of a typical coastal and a detritus food chain in the Westerschelde estuary. Hydrobiological Bulletin 22: 35-41.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Hutchinson, G.E. 1958. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415-427.

Hyslop, E.J. 1980. Stomach contents analysis - a review of methods and their application. Journal of Fish Biology 17: 411-429.

Jacobsson, A., Neuman, E. & Thoreson, G. 1986. The viviparous blenny as an indicator of environmental effects of harmful substances. Ambio 15: 236-238.

James, F.C. & McCulloch, C.E. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? Annual Review of Ecology and Systematics 21: 129-166.

Jaquet, N. & Raffaelli, D. 1989. The ecological importance of the sand goby *Pomatoschistus minutus*. Journal of Experimental Marine Biology and Ecology 128: 147-156.

Jarre, A., Palomares, M.L., Soriano, M.L., Sambilay, V.C.Jr. & Pauly, D. 1991. Some new analytical and comparative methods for estimating the food consumption of fish. ICES marine Science Symposia 193: 99-108.

Jenkins, B.W. & Green, J.M. 1977. A critique of field methodology for determining fish feeding periodicity. Environmental Biology of Fishes 1: 209-214.

Jobling, M. 1986. Mythical models of gastric emptying and implications for food consumption studies. Environmental Biology of Fishes 16: 35-50.

Jones, R. 1974. The rate of elimination of food from the stomachs of haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and whiting *Merlangius merlangus*. Journal du Conseil International pour l'Exploration de la Mer 35: 225-243.

Jones, R. & Hislop, J.R.G. 1978. Further observations on the relation between food intake and growth of gadoids in captivity. Journal du Conseil International pour l'Exploration de la Mer 38: 244-251.

Jongman, R.H.G., Braak, C.J.F. ter & Tongeren, O.F. van 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen. 299 pp.

Keast, A. 1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environmental Biology of Fishes 3: 7-31.

Keddy, P.A. 1989. Competition. Chapman & Hall, London. 202 pp.

Kennedy, C.R. 1975. Ecological animal parasitology. Blackwell Science Publications, Oxford. 163 pp.

Kinne, O. 1984. Diseases of fish: Introduction. In: Kinne, O. (Ed.). Diseases of marine animals. Volume IV: 1-16.

Koter, M. 1962. Helminth parasites in Gobiidae of the Puck Bay. Acta parasitologica polonica 15: 217-227.

Kühl, H. 1961. Nahrungsuntersuchungen an einigen Fischen im Elbe-Mündungsgebiet. Berichte der deutschen wissenschaftlichen Kommissionen für Meeresforschung 16: 90-104.

Kühl, M. 1973. Nahrungsuntersuchungen an einigen Gadiden im Elbe Mündungsgebiet. Archiv für Fischereiwissenschaft 24: 141-149.

Kuhn, T.S. 1970. The structure of scientific revolutions. Second edition. University of Chicago Press, Chicago. 210 pp.

Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). Netherlands Journal of Sea Research 9: 69-85.

Kuipers, B., MacCurrin, B., Miller, J.M., Veer, H.W. van der & Witte, J.IJ. 1992. Small trawls in juvenile flatfish research: their development and efficiency. Netherlands Journal of Sea Research 29: 109-117.

Last, J.M. 1978. The food of three species of gadoid larvae in the eastern English Channel and southern North Sea. Marine Biology 48: 377-386.

Lebour, M.V. 1920. The food of young fish No. III. Journal of the marine biological Association of the United Kingdom 12 : 261-314.

Lee, S.C. 1975. Biology of the sand goby, *Pomatoschistus minutus* (Pallas) (Teleostei, Gobioidei), in the Plymouth area. Ph.D. thesis, University of Bristol.

Le Mao, P. 1986. Feeding relationships between the benthic infauna and the dominant benthic fish of the Rance estuary (France). Journal of the marine biological Association of the United Kingdom 66: 391-401.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton. 120 pp.

Likens, G.E. (Ed.) 1989. Long-term studies in ecology. Springer Verlag, New York. 214 pp.

Lindström, K. 1988. Male-male competition for nest sites in the sand goby, *Pomatoschistus minutus*. Oikos 53: 67-73.

Lorenzen, S. 1974. Die Nematodenfauna der sublitoralen Region der Deutschen Bucht, insbesondere im Titan-abwassergebiet bei Helgoland. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven 14: 305-327.

Lorenzen, S., Prein, M. & Valentin, C. 1987. Mass aggregations of the free-living marine nematode *Pontonema vulgare* (Oncholaimidae) in organically polluted fjords. Marine Ecology- Progress Series 37: 27-34.

Louters, T., Mulder, J.P.M., Postma, R. & Hallie, F.P. 1991.
Changes in coastal morphological processes due to the closure of tidal inlets in the SW Netherlands. Journal of Coastal Research 7: 635-652.

MacArthur, R.H. 1970. Species packing and competitive equilibrium among many species. Theoretical Population Biology 1: 1-11.

Macer, C.T. 1966. Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. Fishery Investigations. Ministry of Agriculture, Fisheries and Food (ser. 2) 24: 1-55.

Macer, C.T. 1967. The food web in Red Wharf Bay (North Wales) with particular reference to young plaice. Helgoländer wissenschaftliche Meeresuntersuchungen 15: 560-573.

Magnhagen, C. 1985. Random prey capture or active choice? An experimental study on prey selection in three marine fish species. Oikos 45: 206-216.

Magnhagen, C. 1988. Changes in foraging as a response to predation risk in two gobiid fish species, *Pomatoschistus minutus* and *Gobius niger*. Marine Ecology - Progress Series 49: 21-26.

Magnhagen, C. 1992. Alternative reproductive behaviour in the common goby, *Pomatoschistus microps*: an ontogenetic gradient? Animal Behaviour 44: 182-184.

Magnhagen, C. & Kvarnemo, L. 1989. Big is better: the importance of size for reproductive success in male *Pomatoschistus minutus* (Pallas) (Pisces, Gobiidae). Journal of Fish Biology 35: 755-763.

Mann, H., 1964. Vorkommen, Verbreitung und Schadwirkung von *Lernaeocera minuta* (T. Scott) (Copepoda parasitica). Veröffentlichungen der Institut für Meeresforschung, Bremerhaven 9: 78-83.

Marchand, J. (in press). The influence of seasonal salinity and turbidity maximum variations on the nursery function of the Loire estuary. Netherlands Journal of Aquatic Ecology.

Markowski, S., 1935a. Die parasitischen Würmer von *Gobius minutus* PALL. des polnischen Balticums. Bulletin de l'Académie des Sciences, Serie B. 2: 251-260.

Markowski, S., 1935b. Uber den Entwicklungszyklus von *Bothriocephalus scorpii* (MULLER 1776). Bulletin de l'Académie des Sciences, Serie B. 2: 1-17.

Mauchline, J. 1980. The biology of mysids and euphausiids. In: Blaxter, J.H.S., Russell, F.S. & Yonge, M. (Eds.). Advances in Marine Biology 18: 1-681.

Mearns, A.J. & Allen, J. 1978. Use of small otter trawls in coastal biological surveys. Southern California Coastal Water Research Project. EPA-600/3-78-083.

Mees, J. & Hamerlynck, O. 1992. Spatial community structure of the winter hyperbenthos of the Schelde estuary, the Netherlands, and the adjacent coastal waters. Netherlands Journal of Sea Research 29: 357-370.

Mees, J., Cattrijsse, A. & Hamerlynck, O. (in press a). Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, southwest Netherlands. Cahiers de Biologie Marine.

Mees, J., Dewicke, A. & Hamerlynck, O. (in press b). Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. Netherlands Journal of Aquatic Ecology.

Mehner, T. 1992. Diet spectra of *Pomatoschistus microps* (Krøyer) and *Pomatoschistus minutus* (Pallas) (Teleostei, Gobiidae) during first weeks after hatching. Zoologische Anzeiger 229: 13-20.

Miller, P.J. 1979. Adaptiveness and implications of small size in teleosts. Symposia of the zoological Society 44: 263-306.

Miller, P.J. 1984. The tokology of gobioid fishes. In: Potts, G.W. & Wootton, R.J. (Eds.). Fish reproduction - Strategies and tactics. Academic Press, London: 119-153.

Miller, P.J. 1986. Gobiidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. & Tortonese, E. (Eds.). Fishes of the North-eastern Atlantic and the Mediterranean, Vol. III. Paris, UNESCO: 1019-1085.

Morawski, M.S. 1978. Winter feeding of the sand goby (*Pomatoschistus minutus* Pallas) in relation to the depth in Gdansk Bay. Kieler Meeresforschungen Sonderheft 4: 122-127.

Moreira, F., Costa, J.L., Almeida, P.R., Assis, C.P. & Costa, M.J. 1991. Age determination in *Pomatoschistus minutus* (Pallas) and *P. microps* (Krøyer) (Pisces: Gobiidae) from the upper Tagus estuary, Portugal. Journal of Fish Biology 39: 433-440.

Morgan, S.G. 1990. Impact of planktivorous fishes on dispersal, hatching, and morphology of estuarine crab larvae. Ecology 71: 1639-1652.

Nagabhushanam, A.K. 1965. On the biology of the commoner gadoids in Manx waters. Journal of the Marine Biological Association of the UK 45: 615-657.

Nellbring, S. 1986. A quantitative and experimental study of goby (*Pomatoschistus* spp.) nests on a shallow soft bottom, northern Baltic proper. Ophelia 25: 15-23.

Nelson, A.L. & Coull, B.C. 1989. Selection of meiobenthic prey by juvenile spot (Pisces): an experimental study. Marine Ecology-Progress Series 53: 51-57.

Niemelä, J. 1993. Interspecific competition in ground-beetle assemblages (Carabidae): what have we learned? Oikos 66: 325-335.

Noort, G.J. van, Creutzberg, F. & Dapper, R. 1984. 'Aurelia'-cruise reports on the benthic fauna of the southern North Sea. Report 8: trawl survey October 1976. Interne Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel. 72 pp. (in Dutch).

Northcott, S.J. 1991. A comparison of circatidal rhythmicity and entrainment by hydrostatic pressure cycles in the rock goby, *Gobius paganellus* L. and the shanny, *Lipophrys pholis* (L.). Journal of Fish Biology 39: 25-33.

Ólafsson, E. 1992. Small-scale spatial distribution of marine meiobenthos: the effects of decaying macrofauna. Oecologia 90: 37-42.

Oliver, M. 1949. Contribución al estudio de la biometría y biología de la faneca, *Gadus luscus* (L.). Boletin del Instituto Español de Oceanografia 15: 1-12.

Olson, R.J. & Mullen, A.J. 1986. Recent developments for making gastric evacuation and daily ration determinations. Environmental Biology of Fishes, 16: 183-191.

Onadeko, C.A. 1992. The food and feeding habits of the sleeper goby, *Batanga lebretonis* (Steindachner) (Pisces: Teleostei: Eleotrididae) in the Lagos Lagoon, Nigeria. Journal of African Zoology 106: 177-189.

Pálsson, O.K. 1980. Über die biologie junger Gadiden der Altersgruppen 0, I und II in isländischen Gewässern. Meeresforschung 28: 101-145.

Parker, N.C. 1984. Chronobiological approach to aquaculture. Transactions of the American Fisheries Society 113: 545-552.

Patterson, K.R. 1985. The trophic ecology of whiting (*Merlangius merlangus*) in the Irish Sea and its significance to the Manx herring stock. Journal du Conseil international pour l'Exploration de la Mer 42: 152-161.

Pearson, T.H. & Rosenberg, R. 1987. Feast and famine: structuring factors in marine macrobenthic communities. In: Gee, J.H.R. & Giller, P.S. (Eds.). Organization of communities: past and present. Blackwell, Oxford: 375-395.

Pennington, M. 1985. Estimating the average food consumption by fish from stomach contents data. Dana 5: 81-86.

Persson, L. 1986. Patterns of food evacuation in fishes: a critical review. Environmental Biology of Fishes 16: 51-58.

Peters, R.H. 1991. A critique for ecology. Cambridge University Press, Cambridge. 366 pp.

Pihl, L. 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Netherlands Journal of Sea Research 15: 419-432.

Pihl, L. 1985. Food selection and consumption of mobile epibenthic fauna in shallow coastal marine areas. Marine Ecology - Progress Series 22: 169-179.

Pihl, L. & Veer, H.W. van der 1992. Importance of exposure and habitat structure for the population density of 0-group plaice, *Pleuronectes platessa* L., in coastal nursery areas. Netherlands Journal of Sea Research 29: 145-152.

Platt, H.M. & Warwick, R.M. 1983. Free-living marine nematodes. Part I British Enoplids. Synopsis of the British Fauna 28: 1-307.

Pomfret, J.R., Elliott, M., O'Reilly, M.G. & Phillips, S. 1991. Spatial and temporal patterns in the fish communities in two UK North Sea estuaries. In: Elliott, M. & Ducrotoy , J.P. (Eds.). Estuaries and coasts: spatial and temporal intercomparisons. Olsen & Olsen, Fredensborg: 277-284.

Poxton, M.G. & Allouse, S.B. 1982. Water quality criteria for marine fishes. Aquacultural Engineering 1: 153-191.

Price, P.W., Slobodchikoff, C.N. & Gaud, W.S. 1984. A new ecology: Novel approaches to interactive systems. Wiley, New York. 515 pp.

Puente, E. 1986. Contribution à la connaissance de la faune ichthyologique démersale côtière au large d'Arcachon. Biologie du Tacaud *Trisopterus luscus* (Linné, 1758): croissance, reproduction, alimentation. Unpubl. thesis, Université de Bordeaux. 157 pp.

Redant, F. 1977. Het epibenthos en de door haar veroorzaakte fluxen. In: Nihoul, J.C. & Polk, P. (Eds.). Project zee (Mathmodelsea) Eindverslag ICWB, Vol. 8: 199-244. (in Dutch).

Reimer, L.W., 1973. Das Auftreten eines fischtrematoden der Gattung *Asymphylodora* LOOSS, 1899, bei *Nereis diversicolor* O.F. MULLER als Beispiel für einen Alternativzyklus. Zoologischer Anzeiger 191: 187-195.

Renkonen, O. 1938. Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. Annales Zoologici Societatis Zoologicae-Botanicae Fennicae 6: 1-231.

Rijnsdorp, A.D., Stralen, M. van & Veer, H.W. van der 1985. Selective tidal transport of North Sea plaice *Pleuronectes platessa* in coastal nursery areas. Transactions of the American Fisheries Society 114: 461-470.

Robb, A.P. 1981. Observations on the food and diel feeding behaviour of pelagic 0-group gadoids in the northern North Sea. Journal of Fish Biology 18: 183-194.

Robb, A.P. & Hislop, J.R.G. 1980. The food of five gadoid species during the pelagic 0-group phase in the northern north Sea. Journal of Fish Biology 16: 199-217.

Robin, J.P. & Marchand, J. 1986. Preliminary observations on the feeding activity of fishes during tidal and diel cycles in the Loire estuary: the bib *Trisopterus luscus* L. 1758. P.S.Z.N.I.: Marine Ecology 7: 181-189.

Roff, J.C., Hopcroft, R.R., Clarke, C., Chisholm, L.A., Lynn, D.H. & Gilron, G.L. 1990. Structure and energy flow in a tropical neritic planktonic community off Kingston, Jamaica. In: Barnes, M. & Gibson, R.N. (Eds.). Trophic relationships in the marine environment. Proceedings of the 24th European Marine Biology Symposium. Aberdeen University Press, Aberdeen: 266-280.

Rogers, S.I. 1988a. Reproductive effort and efficiency in the female common goby, *Pomatoschistus microps* (Krøyer)(Teleostei: Gobioidei). Journal of Fish Biology 33: 109-119.

Rogers, S.I. 1988b. The seasonal partitioning of energy in an estuarine fish, the common goby, *Pomatoschistus microps* Krøyer. Journal of Fish Biology 33 Suppl. A: 45-50.

Ross, S.T. 1986. Resource partitioning in fish assemblages: A review of field studies. Copeia 1986: 352-388.

Roughgarden, J. 1983. Competition and theory in community ecology. The American Naturalist 122: 583-601.

Sainsbury, K.J. 1986. Estimation of food consumption from field observations of fish feeding cycles. Journal of Fish Biology 29: 23-36.

Santos, P.T. 1989. On the food of the pouting (*Trisopterus luscus* L.) in the north coast of Portugal. Publicações do Instituto de Zoologia 'Dr. Augusto Nobre' 207: 1-15.

Schmidt-Moser, R. & Westphal, D. 1981. Predation of *Pomatoschistus microps* Krøyer and *P. minutus* Pallas (Gobiidae, Pisces) on macro- and meiofauna in the brackish fjord Schlei. Kieler Meeresforschungen Sonderheft 5: 471-478.

Schmitt, R.J. & Holbrook, S.J. 1990. Population responses of surfperch released from competition. Ecology 71: 1653-1665.

Schoener, T.W. 1983. Field experiments on interspecific competition. The American Naturalist 122: 240-285.

Scott, T. 1902. Observations on the food of fishes. Annual Reports of the Fisheries Board of Scotland 20: 486-538.

Sharma, J. 1985. A study of the nematode fauna of three estuaries in The Netherlands. Ph.D. thesis, State University of Gent.

Sievers, U. 1989. Nahrungsökologische Untersuchungen an Seehunden (*Phoca vitulina*, Linné 1758) aus dem Schleswig-holsteinischen Wattensee. Zoologische Anzeiger 222: 449-460.

Simberloff, D. 1983. Competition theory, hypothesis-testing, and other community ecological buzzwords. The American Naturalist 122: 626-635.

Sissenwine, M.P. & Daan, N. 1991. An overview of multispecies models relevant to management of living resources. ICES marine Science Symposia 193: 6-11.

Smol, N. 1986. Rol van het meiozoobenthos in de Oosterschelde. Internal Report Delta Institute for Hydrobiological Research. Yerseke, The Netherlands. 151 pp. (in Dutch).

Sobral, M. & Rebordão, E. 1982. Contribution à l'étude du tacaud - *Trisopterus luscus* (Linnaeus, 1758) de la côte portugaise. International Council for the Exploration of the Sea CM 1982/G: 15.

Sokal, R.R. & Rohlf, F.J. 1981. Biometry. Second edition. W.H. Freeman, San Francisco. 859 pp.

Sugihara, G., Garcia, S., Gulland, J.A., Lawton, J.H., Maske, H., Paine, R.T., Platt, T., Rachor, E., Rothschild, B.J., Ursin, E.A. & Zeitschel, B.F.K. 1986. Ecosystems dynamics, Group Report. In: May, R.M. (Ed.). Exploitation of marine communities. Springer-Verlag, Berlin: 131-153.

Tallmark, B. & Evans, S. 1986. Substrate-related differences in antipredator behaviour of two gobiid fish species and the brown shrimp, and their adaptive value. Marine Ecology - Progress Series 29: 217-222.

Thorman, S. 1982. Niche dynamics and resource partitioning in a fish guild inhabiting a shallow estuary on the Swedish west coast. Oikos 39: 32-39.

Thorman, S. & Wiederholm, A.-M. 1983. Seasonal occurrence and food resource use of an assemblage of nearshore fish species in the Bothnian Sea, Sweden. Marine Ecology - Progress Series 10: 223-229.

Thorman, S. & Wiederholm, A.-M. 1984. Species composition and dietary relationships in a brackish shallow water fish assemblage in the Bothnian Sea, Sweden. Estuarine, Coastal and Shelf Science 19: 359-371.

Thorman, S. & Wiederholm, A.-M. 1986. Food, habitat and time niches in a coastal fish species assemblage in a brackish water bay in the Bothnian Sea, Sweden. Journal of Experimental Marine Biology and Ecology 95: 67-86.

Tiews, K. 1990. 35-Jahres-Trend (1954-1988) der Häufigkeit von 25 Fisch- und Krebstierbeständen an der deutschen Nordseeküste. Archiv für Fisherei-wissenschaften 40: 39-48.

Ursin, E., Pennington, M., Cohen, E.B. & Grosslein, M.D. 1985. Stomach evacuation rates of Atlantic cod (*Gadus morhua*) estimated from stomach contents and growth rates. Dana 5: 63-80.

Vanreusel, A. 1990. Ecology of free-living marine nematodes in the Voordelta (Southern Bight of the North Sea). I. Species composition and structure of the nematode communities. Cahiers de Biologie Marine 31: 439-462.

Vanreusel, A. 1991. Ecology of free-living marine nematodes in the Voordelta (Southern Bight of the North Sea). II. Habitat preferences of the dominant species. Nematologica 37: 343-359.

Veer, H.W. van der 1986. Immigration, settlement, and density-dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western wadden Sea. Marine Ecology - Progress Series 29: 223-236.

Vincent, T.L. & Brown, J.S. 1988. The evolution of ESS theory. Annual review of Ecology and Systematics 19: 423-443.

Vincx, M. 1986. Free-living marine nematodes from the Southern Bight of the North Sea. Ph.D. thesis, State University of Gent.

Vlas, J. de 1985. Secondary production by siphon regeneration in a tidal flat population of *Macoma balthica*. Netherlands Journal of Sea Research 19: 147-164.

Walter, G.H. 1991. What is resource partitioning? Journal of theoretical Biology 150: 137-143.

Warburton, K. & Blaber, S.J.M. 1992. Patterns of recruitment and resource use in a shallow-water fish assemblage in Moreton Bay, Queensland. Marine Ecology - Progress Series 90: 113-126.

Warwick, R.M. & Clarke, K.R. 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. Marine Ecology Progress Series 92: 221-231.

Washington, H.G. 1984. Diversity, biotic and similarity indices. A review with special relevance to aquatic ecosystems. Water Research 18: 653-694.

Webb, C.J. 1980. Systematics of the *Pomatoschistus minutus* complex (Teleostei: Gobiidae). Philosophical Transactions of the Royal Society (B) 291: 201-241.

Wharfe, J.R., Wilson, S.R. & Dines, R.A. 1984. Observations on the fish populations of an east coast estuary. Marine Pollution Bulletin 15: 133-136.

Wieser, W. 1953. Beziehungen zwischen Mundhölengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Arkiv för Zoologi 4: 439-484.

Wootton, R.J. 1990. Ecology of teleost fishes. Chapman & Hall, London: 1- 404.

Worobec, M.N. 1984. Field estimates of the daily ration of winter flounder, *Pseudopleuronectes americanus* (Walbaum), in a southern New England salt pond. Journal of Experimental Marine Biology and Ecology 77: 183-196.

Zander, C.D. 1990. Prey selection of the shallow water fish *Pomatoschistus minutus* (Gobiidae, Teleostei) in the SW Baltic. Helgoländer Meeresuntersuchungen 44: 147-157.

Zander, C.D. & Hagemann, T. 1987. Predation impact and ecological efficiency of *Pomatoschistus* spp. (Gobiidae, Pisces) from a clay/sand ecotone of the Western Baltic sea. Zoologische Anzeiger 218: 33-48.

Zaret, T.M. & Rand, A.S. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336-342.

APPENDIX

List of the assigned weights and the Length-Ash free Dry Weight (ADW) regressions of the prey found in the stomachs of *Pomatoschistus minutus* and *P. lozanoi*. All lengths (L), standardlengths (SL), total lengths (TL) and carapax widths (CB) are in millimeter, all weights (ADW) and assigned weights are in milligram ADW.

Foraminifera: assigned value 0.001

Nematoda: assigned value 0.003

Bivalvia
- bivalve material: weighed value
- bivalve siphon: $\ln ADW = 0.043 \ln L + 0.815$
- bivalve species: $\ln ADW = 2.817 \ln L - 4.052$

Polychaeta
- Errantia
  - *Sthenelais boa*: $\ln ADW = 1.785 \ln L - 4.389$
  - *Eteone* species: $\ln ADW = 1.530 \ln L - 5.717$
  - *Anaitides* species: $\ln ADW = 1.674 \ln L - 5.882$
  - *Nephtys* species: $\ln ADW = 2.489 \ln L - 7.139$

    all other errant species: see *Anaitides*

- Sedentaria
  - *Lanice* radiole crowns: weighed value
  - Spionidae species: $\ln ADW = 1.831 \ln L - 6.030$
  - *Capitella capitata*: $\ln ADW = 2.051 \ln L - 6.354$
  - *Pectinaria koreni*: $\ln ADW = 2.689 \ln L - 6.918$
  - *Lanice conchilega*: $\ln ADW = 2.181 \ln L - 6.918$

    all other sendentarian species: see *Lanice*

Oligochaeta: $\ln ADW = 1.831 \ln L - 6.030$

Crustacea
- Ostracoda: assigned value 0.014

- Copepoda

Calanoida
    copepodite: assigned value 0.005
    adult: assigned value 0.016
Harpacticoida
    copepodite: assigned value 0.001
    small adult species: assigned value 0.002
    large adult species: assigned value 0.004
Cyclopoida
    adult: assigned value 0.016

Cirripedia
    nauplii: assigned value 0.001
    cypris larvae: assigned value 0.014
    cirripeds arm: $\ln \mathrm{ADW} = 2.863 \ln \mathrm{L} - 5.857$

Mysidacea
    Gastrosaccus spinifer: $\ln \mathrm{ADW} = 2.873 \ln \mathrm{SL} - 5.896$
    Gastrosaccus sanctus: $\ln \mathrm{ADW} = 2.994 \ln \mathrm{SL} - 6.120$
    Schistomysis spiritus: $\ln \mathrm{ADW} = 2.601 \ln \mathrm{SL} - 5.237$
    Schistomysis kervillei: $\ln \mathrm{ADW} = 2.931 \ln \mathrm{SL} - 5.898$
    Mesopodopsis slabberi: $\ln \mathrm{ADW} = 2.867 \ln \mathrm{SL} - 6.107$

    Siriella armata: see *Gastrosaccus sanctus*
    Neomysis integer: see *Schistomysis kervillei*
    all other mysids: see *Schistomysis spiritus*

Cumacea: $\ln \mathrm{ADW} = 2.525 \ln \mathrm{TL} - 6.078$

Isopoda: $\ln \mathrm{ADW} = 2.863 \ln \mathrm{TL} - 5.857$

Amphipoda
    Bathyporeia species: $\ln \mathrm{ADW} = 4.563 \ln \mathrm{TL} - 8.674$

    all other amphipods: $\ln \mathrm{ADW} = 2.863 \ln \mathrm{TL} - 5.857$

Decapoda
    Caridea
        zoeae: assigned value 0.175
        postlarvae: assigned value 0.238
        adult: $\ln \mathrm{ADW} = 3.321 \ln \mathrm{TL} - 7.684$

Anomura

Pagurus bernhardus: weighed value

Galathea megalopae: assigned value 0.669

Brachyura

Cancer pagurus megalopae: assigned value 0.669

Liocarcinus species

zoeae: assigned value 0.152

megalopae: assigned value 0.189

adult: lnADW = 3.247 lnCB - 4.489

Carcinus species

zoeae: assigned value 0.050

megalopae: assigned value 0.081

adult: lnADW = 3.164 lnCB - 3.967

all other brachyurans: see *Carcinus* species

Echinodermata

Ophiuroidea arm fragments: weighed value

Chaetognatha

Sagitta elegans: assigned value 0.500

Pisces

fish eggs: assigned value 0.025

Syngnathus rostellatus: lnADW = 3.139 lnSL - 10.420

Pomatoschistus minutus: lnADW = 3.460 lnSL - 7.851

Pomatoschistus lozanoi: lnADW = 3.446 lnSL - 7.842

all other fishes: see *Pomatoschistus minutus*