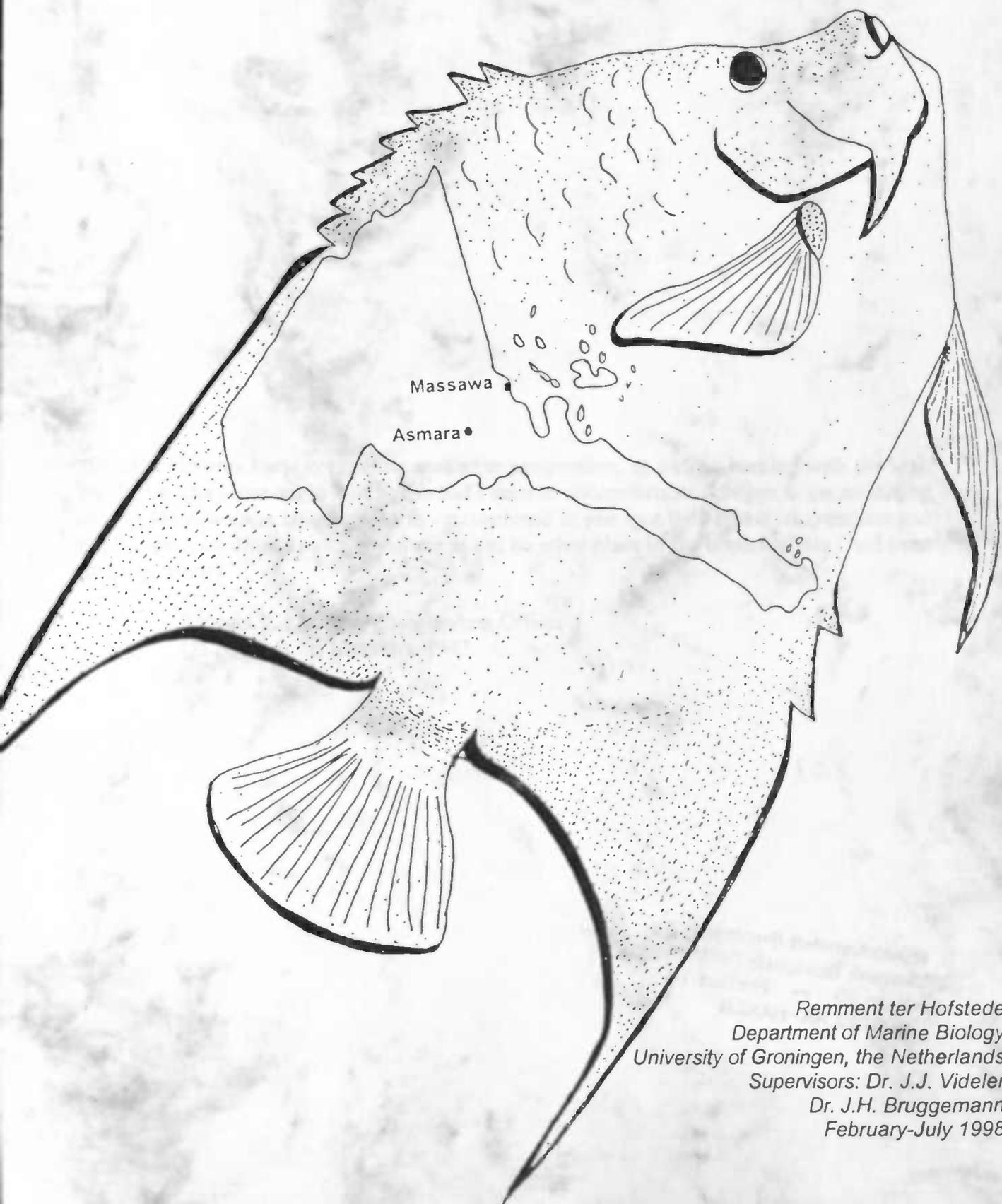


Feeding ecology of the angelfish species
Pomacanthus asfur and *Pomacanthus*
maculosus.



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Dr. J.H. Bruggemann
February-July 1998

"In a few minutes I was completely soaked in perspiration, as well as burning with the heat. Neither in Khartoum nor in Port Sudan had I been so uncomfortable. I began to get an inkling of why Massawa was unique on earth - it combined in one spot the highest temperatures and the highest humidities known anywhere as did no other place in the tropics. What I had been told was correct."

- Captain E. Ellsberg, Commanding Officer
US Naval Base, Massawa, 1942

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Abstract

The feeding ecology of the angelfish species *Pomacanthus maculosus* and *Pomacanthus asfur* was studied at the coral reefs of Massawa in Eritrea, a country situated at the west-coast of the Red Sea. These angelfishes are active during the day and feed mainly by nipping the substrate within a small home range. The feeding activity in terms of bite rate was investigated during different parts of the day for both species, but the intraspecific variation was too high to draw conclusions about variation in feeding activity during the day. Looking at the entire day, *P. asfur* has a higher bite rate than *P. maculosus*.

Stomach contents were analysed in order to determine diet and interspecific overlap. Sponges and algae made up the largest part of their diverse diets, so both species can be regarded omnivorous. The stomach contents of *P. maculosus* were clotted in packages, those of *P. asfur* consisted of pulverised material.

The digestive tracts of these angelfishes are structurally similar. Their fairly strong stomach, long intestine and terminal sac makes them well adapted to their omnivorous way of feeding. *P. asfur* has a relatively longer intestine than *P. maculosus* and together with the fact that its stomach content is already more pulverised, it seems to have a higher capacity for nutrient absorption than *P. maculosus*.

Contents

| | page |
|----------------------------|---------|
| Title page..... | 1 |
| Abstract..... | 2 |
| Contents..... | 3 |
| Introduction..... | 4 - 8 |
| Fisheries..... | 4 |
| Pomacanthidae..... | 6 |
| Main questions..... | 8 |
| Materials and Methods..... | 9 - 12 |
| Study site..... | 9 |
| Feeding activity..... | 11 |
| Dissections..... | 12 |
| Stomach contents..... | 12 |
| Results..... | 13 - 17 |
| Feeding activity..... | 13 |
| Dissections..... | 15 |
| Stomach contents..... | 16 |
| Discussion..... | 18 - 19 |
| Feeding activity..... | 18 |
| Dissections..... | 18 |
| Stomach contents..... | 19 |
| Conclusions..... | 20 |
| References..... | 21 - 22 |
| Acknowledgements..... | 23 |
| Appendix..... | 24 - 32 |

Introduction

Fisheries

Growing human populations with inherent needs for food and income have driven the development and expansion of fisheries on tropical coasts. Therefore fishing is the most widespread human exploitative activity on coral reefs, but other human activities also play a role in disturbances on the reef. Examples of these other activities are coral mining, in which corals are extracted for use as raw material in lime production, degradation of coastal terrestrial vegetation patterns in favour of agriculture, which causes sedimentation of the reefs, and unregulated tourism, inducing destruction of the corals reefs by collecting sea life and anchoring boats (Öhman *et al.*, 1993).

Fishing for food can cause considerable damage to a reef: indirectly by the removal of the fish and directly by the manner of catching the fish.

The removal of fish upsets the balance in a reef ecosystem of which the existing condition may be a result of a long evolutionary process. A change in fishing intensity of specific species is in general correlated with substantial changes in an ecosystem (Jennings & Lock, 1996). It is a fact that successful fishing leads to a reduction in the abundance, biomass and mean size of species targeted by fisheries (Jennings & Polunin, 1996).

The most favourable species for consumption are carnivorous fish, which yield a high amount of food. These species are highest in the food chain and therefore, their decrease has shown to be the most readily detectable effect of fishing pressure (Russ, 1991). When these favoured species become extinct because of extensive fishing, there will be a development in the reef composition and smaller species from lower trophic levels, like herbivorous fish, will begin to dominate. These herbivorous fish have profound influences on the rates of reef accretion. Their grazing activities may clear space for coral settlement and enhance the survival and growth of young coral colonies (Bakus, 1966). If the fisheries pressure on this trophic level becomes high, as a consequence of extirpation of carnivorous fish, it might result in a large reduction of the herbivorous fish, too. The lack of these grazers enables algae to overgrow the coral, causing a destruction of the reef ecosystem. It has a retrospective effect on fisheries, because the loss of structural complexity leads to disruption of the ecological processes that are responsible for fish production, and finally to a reduction in fish biomass (Jennings & Polunin, 1996).

The direct way in which corals get destructed by fisheries for nourishment is the manner of catching the fish. Blast fishing ("fishing" with explosives), chemical fishing (poisoning the fish) and many netting techniques all cause irreversible damage to the substrate and will therefore lead to a redistribution of exploitable fish biomass or reduce the potential fish production from reef ecosystems (Williams, 1991).

Besides fishing for food, fishing for trade in aquarium fish also occurs and it can have the same destructive effects on reef ecosystems. Corals are often broken during the capture of the fish, for example as a result of the use of the barrier-net technique. Using this technique, the fish are captured by placing a plumbed net around the fish's refuge, followed by driving the fish out of its hideout into the barrier-net by either rocking the hiding place back and forth or banging it with an iron bar (see fig. 1).

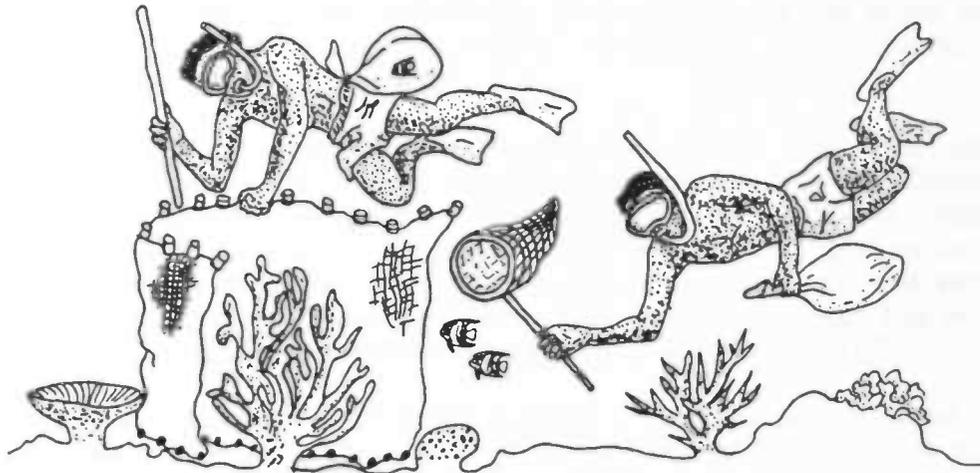


Figure 1: Fishermen use the barrier-net technique for catching ornamental fish.

This collection of ornamental fish can be an important economic activity. In Sri Lanka for example, the ornamental fish exports rate third highest, after prawns and lobster, in terms of the volume and value of fishery exports. Therefore, the damage to the reefs can be extensive (Baldwin, 1991).

All these previously described effects of fisheries may lead to a great loss of fish production and they show little evidence of being reversible within a short-time scale (years). These effects of fishing on reefs suggest that mankind cannot afford to ignore the tight interactions between fishes and their ecosystems (Hughes, 1994).

In Eritrea, an African country at the west-coast of the Red Sea, trade in aquarium fish also occurs, though less extensive than in Sri Lanka. Still, the ornamental fish trade is a rising business. Therefore, it is important to stay alert, for example by studying the target species intensively in order to obtain information about their ecology and take that into account by executing a policy strategy for sustainable fishing.

Pomacanthidae

Angelfish (Pomacanthidae) are examples of ornamental fish that are frequently caught in Eritrea by aquarium fish trade companies.

The family of angelfishes is among the most colourful and widely recognised of all reef fishes, so it is not surprising that many species of this family have common names like queen, king and emperor angelfish.

Angelfishes are strongly laterally compressed, have high bodies, are round in profile and have continuous dorsal fins. They are brightly coloured and have a strongly developed preopercular spine (Smith, 1986).

The family of angelfishes has got a circumtropical distribution, still it is a relatively small group with only seven widely recognised genera: *Centropyge*, *Chaetodontoplus*, *Euxiphipops*, *Genicanthus*, *Holacanthus*, *Pomacanthus* and *Pygoplites* (Fraser-Brunner, 1933). Paralleling the relatively few genera, there are also relatively few species, with a total of 74. *Centropyge* is by far the most speciose genus, with 29 recognised species; at the other extreme, *Pygoplites* is monotypic, containing only one species. The remaining five genera consist of less than a dozen species each (Randall & Yasuda, 1979).

The amount and kind of sexual dimorphism exhibited in Pomacanthids varies widely, from genera that are known to be monomorphic, *Euxiphipops* and *Pomacanthus*, to a genus of which all species exhibit pronounced sexual differences in size, shape, and coloration, *Genicanthus* (Thresher, 1984).

Juveniles of many of the larger species have a different colour pattern from the adults, mostly blue with white markings (Randall, 1983).

Angelfishes are considered to have a strong seasonal change in spawning activity. In temperate regions, spawning characteristically occurs during the warmest months of the year, whereas closer to the equator spawning is also seasonal, but seems to peak when water temperatures are rising. During the season, spawning occurs daily and not according to a lunar cycle.

There are several general features regarding spawning behaviour by angelfish. It occurs at dusk, slightly off the bottom and ends with a spiraling or straight, relatively slow, ascent into the water column to release eggs and sperm. Spawning always involves a single pair of fish, although males of many angelfish species do spawn successively with several females. There are no reports of group spawning or even cheating by smaller males (Thresher, 1984).

Pomacanthids are considered to have territories where they forage during the day and where they find shelter between the rocks for the night.

Most angelfish are considered to be omnivorous, feeding on a wide variety of algae, corals, sponges and other small invertebrates (Hourigan, 1989).

The species studied in this project, the Arabian Angelfish *P.asfur* and the Yellowbar Angelfish *P.maculosus*, belong to the genus *Pomacanthus* and are closely related. They are examples of species that are caught in Eritrea for trade in aquarium fish. The yield prices are about US\$ 75-105 for *P.maculosus* and US\$ 90-120 for *P.asfur*.

Adults can be recognised by a yellow bar on their blue body. The two species can be distinguished by size and colour: *P.maculosus* grows up to 50 cm and is light blue in body colour; *P.asfur* is smaller (up to 35 cm) and black with a bluish glow (Randall, 1983) (see fig. 2).

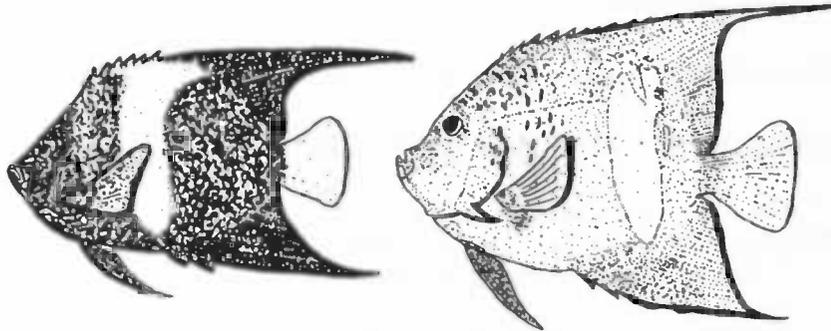


Figure 2: Morphology of *Pomacanthus asfur* (left) and *Pomacanthus maculosus* (right).

Gause's principle states that two species that are identical in their requirements (same niche), such as type of habitat and diet, cannot coexist indefinitely. In general, competition occurs whenever two species interact and each species affects the ability of the other to reproduce, survive, and increase its population.

Of the many parameters limiting the abundance of reef fishes, food and space have been considered to be most important (Doherty & Williams, 1988). Jones (1968) for example, studied the variables separating the family *Acanthuridae* ecologically; habitat preference, foraging methods, diet, and morphological specialisations for feeding were found to be most important. A similar set of variables might also separate the ecological requirements of the species in the large and diverse family of Pomacanthidae. These kind of comparative studies on pomacanthids have only limited been conducted on the genera *Centropyge*, *Genicanthus*, *Holacanthus* and *Pomacanthus*, and it appeared that food and space were not limiting resources (Sakai & Kohda, 1995; Howe, 1993; Pérez-España & Abitia-Cárdenas, 1996; Hourigan *et al.*, 1989).

Scientists who have worked with pomacanthids agree that species belonging to the genera *Pomacanthus* are grazers, and that the most important food sources are sponges and seaweeds (Reynolds & Reynolds, 1976; Hourigan *et al.*, 1989).

Main questions

This study is part of a larger project to provide ecological and biological information that can be used for future management of ornamental fish in Eritrea. It focuses on the angelfish species *P.asfur* and *P.maculosus*, which are abundant on the Eritrean reefs. No studies of their population dynamics or the impacts of exploitation have been conducted before, even studies of their biology are scarce. Considering the fact that these species are abundant in Eritrea, it is useful to perform research on them as a starting point for ornamental fisheries management in Eritrea. In order to obtain a basic idea of the life of these two angelfish species, the behaviour and distribution of both species (Haydar, 1998), as well as their feeding ecology were investigated.

This paper focuses on feeding ecology and the aim is answering the following questions:

- 1) What is the feeding activity of *Pomacanthus asfur* and *P.maculosus* during the day in terms of bite rate?
- 2) What are the similarities and differences in the structure of the digestive tract of *P.asfur* and *P.maculosus* and how does this relate to their diet?
- 3) What is the diet composition of *P.asfur* and *P.maculosus* determined on the basis of stomach analysis and observations of their feeding behaviour?

Materials and Methods

Study site

Fieldwork was conducted around Massawa (15° 39' N, 39° 28' O), which is the main harbour of Eritrea (see figure 3).

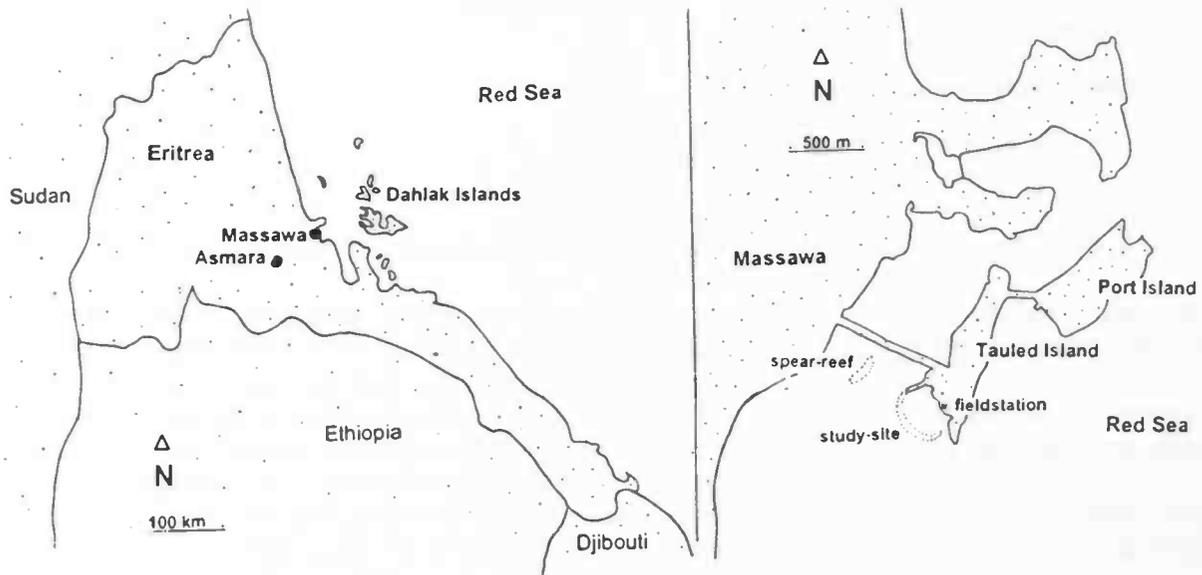


Figure 3: Overview of the situation of the study site.

The fish diversity and amounts are very high in the waters around Massawa and about 527 species of fish have been recorded by the Ministry of Fisheries.

The study-site also supported a large variety of reef fish, which included predatory fish such as groupers (*Serranidae*), snappers (*Lutjanidae*), jacks (*Carangidae*), emperors (*Lethrinidae*) and breams (*Sparidae*), and grazers such as parrotfish (*Scaridae*), rabbitfish (*Siganidae*), surgeonfish (*Acanthuridae*), butterflyfish (*Chaetodontidae*), angelfish (*Pomacanthidae*), wrasses (*Labridae*) and damselfish (*Pomacentridae*). A total of 88 fish species has been recorded on the study-site during the period of research (see appendix 1).

The study site was situated on an elongated coral reef in front of the fieldstation of the Department of Marine Biology and Fisheries of the University of Asmara, Eritrea (see figure 4).

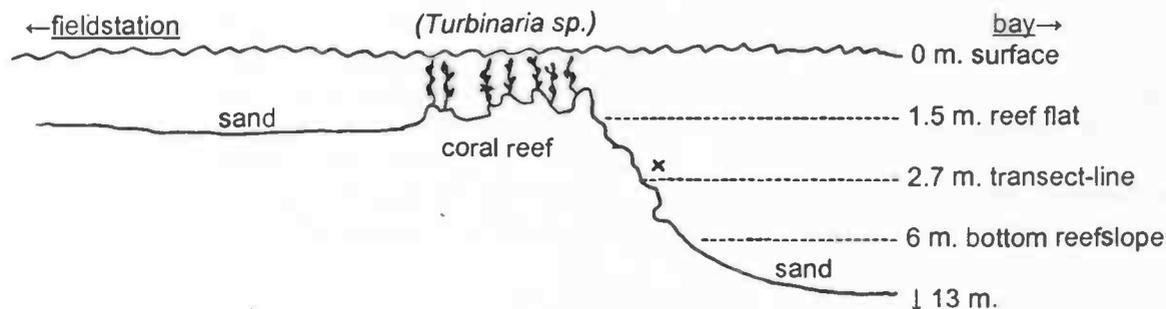


Figure 4: Constitution of the reef where the study site was situated.

This reef consists of a small and fairly steep slope, going from about 0.5 meters (neap tide, 1.5 meters spring tide) at the reef flat to 6 meters deep. At this depth, it changes into a sandy plain, with a maximum depth of 13 meters in the centre of the bay.

The reef flat consists mainly of coarse rubble and small rocks of coral. In the winter season, the reef flat is covered with the macro-algae *Turbinaria sp.* When the temperature rises during springtime, the *Turbinaria sp.* disappears completely.

The reef slope is composed of big rocks of dead coral with a low cover of living coral. This small extent of living coral is probably due to a low light intensity caused by a high sedimentation rate. The visibility varies between only 2 and 8 meters.

Water temperatures range from 28 °C in winter to 38 °C in summer. During the observation period, the water temperature rose from 28 °C at the end of February to 33 °C in the beginning of June.

An observation area was demarcated by placing a permanent transect line of 250 meters along the reef slope. It was placed at an equal depth of approximately 2 meters (during low tide).

Feeding activity

All observations on the feeding behaviour were made during the months April to June 1998. The observations were performed while diving with SCUBA-gear, and all notes were made on PVC sheets. Because the *P.maculosus* and *P.asfur* are not easily scared, behavioural observations at a close range (<1 m) were possible.

Individuals of *P.asfur* were easily distinguished by their size and the place where they were situated on the reef. Individuals of *P.maculosus* were identified likewise, supplemented by the unique bar-pattern on their bodies.

Body size was estimated visually to the nearest 0.5 centimetre in total length. Gender was not determined, due to the monomorphic appearances and a lack of knowledge about social behaviour.

Days were divided into four successive periods of observation in order to investigate if the feeding activity varies during the day: morning starting at sunrise (7.00-10.00 h), around noon (10.00-13.00 h), afternoon (13.00-16.00 h), and early evening till sunset (16.00-19.00 h). During the night (19.00-7.00 h) no observations were conducted since the concerning angelfishes were sleeping in caves.

An observation period lasts 60 minutes and the total number of bites was recorded for each 1 minute interval. Preceding every observation period, the fish was allowed 3 minutes habituation before recording its behaviour.

In total, the manner of feeding and the feeding activity of 6 *P.asfur* individuals and 5 of the species *P.maculosus* was observed. The feeding activity was compared in terms of bite rate between individuals and species for the entire day and its 4 successive parts, by performing a Single Factor ANOVA.

To check whether the bite rate is dependent on the size of the fish, the correlation of bite rates and total body lengths of all observed individuals was determined.

Plans were made to look in the field at the sizes of the bites of both species. In order to determine if their diet varies during the day, the intention was to determine whether the fish show preference for specific food-items.

Dissections

Fish were collected at the 14th, 26th and 27th of May 1998 on a reef adjacent to the one where behavioural studies were conducted (see figure 3). This reef was situated at a depth of 2-6 meters and resembled the study site.

Adult fish were captured between 12.00h and 13.00h using an elastic band powered speargun (the Beuchat Baby) and basic diving equipment. The spear was shot through the muscles of the dorso-ventral part of the body, this way the interior of the fish stayed intact. Subsequently, the speared fish were put on ice, frozen to death. In total, 9 individuals (4 males, 5 females) of the species *P.maculosus* and 2 males of *P.asfur* were caught for dissection. They were all dissected within 4 hours after being caught.

A description of the digestive system was made from the beginning of the stomach to the anus and included the measuring and weighing of the different parts of the digestive tract (see appendix 2). The dry-weights were determined after drying the material in a stove for one week at 60 °C.

The length of each digestive tract and its separate parts (stomach, intestine and terminal sac) were compared with the total length of the accompanying fish.

The wet weights of the digestive tract and its three separate parts were compared with the wet body weight of the fish.

Stomach contents

The contents of the different parts of the digestive tract of all dissected fish were conserved in formaldehyde and transported to Groningen, the Netherlands. After transport, the stomach contents of 6 *P.maculosus* and 2 *P.asfur* individuals could be analysed. The stomach contents of the other three dissected fishes were no longer usable after transport.

Each sample was spread out in a Petri-dish, which was equipped with a grid composed of 0.25 cm² blocks. The contents were scored in duplo at 100 intersections of the gridlines with the use of a 10x stereoscopic microscope.

The in duplo acquired data from the stomach contents were averaged and are given in a table. Differences in diet between the individuals of both species were checked by use of a Single Factor ANOVA.

Before presenting them graphically, all food items were divided into the categories Sponges, Green-, Brown-, and Red Algae, Unidentified (everything that could not be recognised), and Other (unidentified algae and small animals other than sponges).

To inquire if there were differences in stomach contents between species and gender, the categorised data were grouped into *P.asfur male*, *P.maculosus all*, *P.maculosus male* and *P.maculosus female* (there were no females of *P.asfur* dissected)(see table 5 in appendix 5). These groups are also presented graphically and analysed by using a Single Factor ANOVA on the original data (not categorised).

From the intestine and terminal sac samples respectively 6 (4 *P.maculosus*; 2 *P.asfur*) and 3 (2 *P.maculosus*; 1 *P.asfur*) samples were usable after transport. The samples of the contents of intestine and terminal sac all appeared to be too far digested to be investigated as thoroughly as the stomach contents, so they were just roughly examined.

Results

Feeding activity

When feeding, the fish protrudes its mouth and nips off the substrate very quickly. During every bite, it moves its body a bit forward towards the substrate. No differences were observed between the two species. Both species fed mainly in downward position, but didn't seem to mind to eat in an upward position occasionally.

Unfortunately, due to a time-shortage the size of the bites was not observed, neither was looked in the field at what kind of food items the two angelfish species ate throughout the day.

Figure 5 shows the total numbers of bites per hour at different parts of the day for all observations of *P.asfur* and *P.maculosus*. The bite rates in different parts of the day differ greatly among individual fish. There is a high intraspecific variation for several parts of the day (Single Factor ANOVA, see table 2 in appendix 2). Therefore the bite rates in the different parts of the day of the individuals cannot be compared with each other.

Furthermore, there seems to be an interspecific variation in feeding activity in terms of bite rate. Looking at the entire day, the bite rates of *P.asfur* are higher than the bite rates of *P.maculosus* (Student's t-Test: $p = 0.02$; $\alpha = 0.05$).

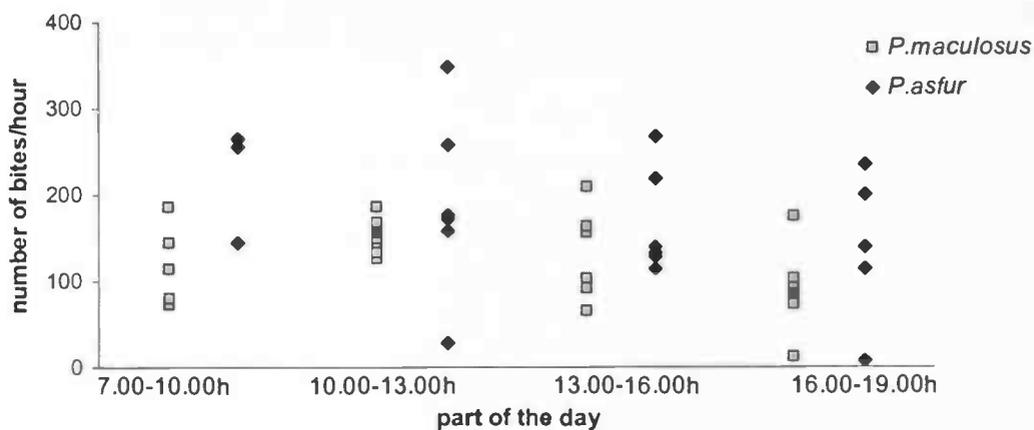


Figure 5: Bite rates of all individuals of *P.asfur* ($n=6$; 20h) and *P.maculosus* ($n=5$; 25h) throughout the day.

Figure 6 displays the average bite rate of every observed individual of both species compared with their total length. The individuals of the species *P.asfur* show large differences in their average bite rate (93 to 277 bites per hour), although the sizes of the individuals vary only moderately (14-16 cm). The average bite rates of *P.maculosus* do not vary much (86-128 bites per hour) while fish size varies more (16-20 cm). Neither of the two species has a bite rate that correlates with the fish length (*P.asfur*: $r=0.1529$; $r_{0.05}=0.811$; $n=6$; *P.maculosus*: $r=0.3663$; $r_{0.05}=0.878$; $n=5$).

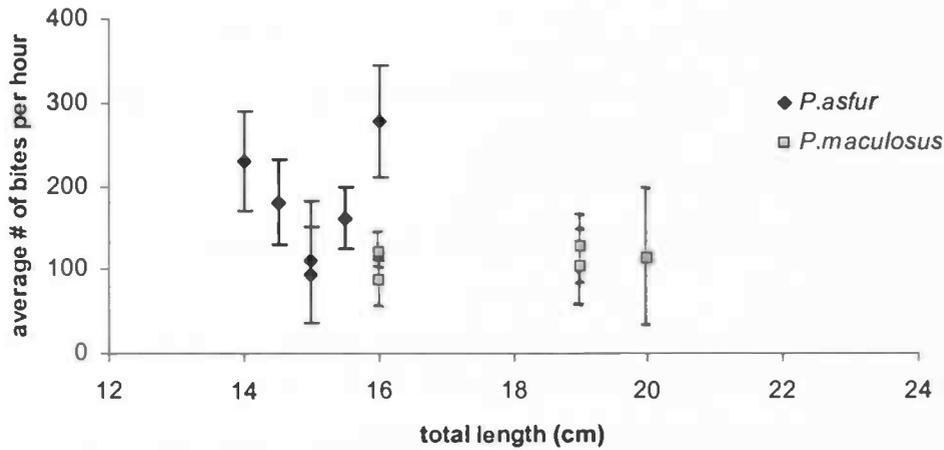


Figure 6: Average bite rate versus total length for all individuals of *P.asfur* ($n=6$; 20h) and *P.maculosus* ($n=5$; 25h).

Dissections

Structurally, the digestive tracts of both angelfish species appear to be similar and a schematic drawing is given in figure 7. They both have a well-defined stomach with strong walls. At the junction of the stomach and intestine, they have a pyloric caecum, which consists of several sacs and it contains fatty secretions. The intestine is very long and at the end shifts into an expanded region that forms a terminal sac.

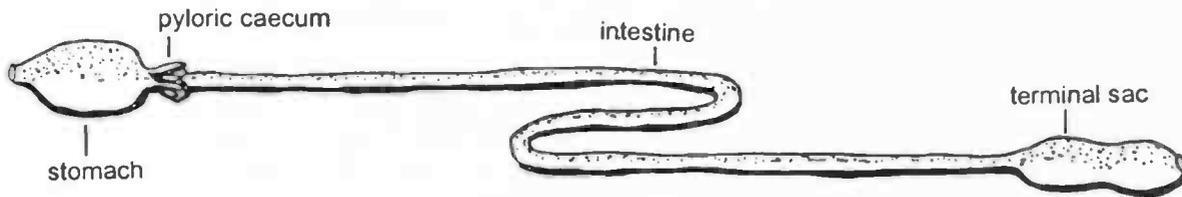


Figure 7: Schematic drawing of the digestive tract of *P.asfur* and *P.maculosus*.

Table 3 in appendix 3 contains all the acquired data of the dissection of all speared fish. The data cover size and weight of the fish, the digestive tracts and its separate parts, and their contents.

After analysing all these data, the two species only appear to differ in the length of the intestine (see table 4 in appendix 4). In figure 8, the relative length of the intestine is plotted against the total length of the fish.

$$\text{relative length of the intestine} = \text{length of the intestine} / \text{total fish length}$$

The graph shows clearly that the species *P.asfur* has a longer intestine in relation to the body length than the species *P.maculosus* (Student's t-test: $p = 0.02$; $\alpha = 0.05$).

The relative length of the intestine of *P.asfur* is $5.4 (\pm 0.3)$ times the total body length and $3.9 (\pm 0.5)$ times the total body length for *P.maculosus*.

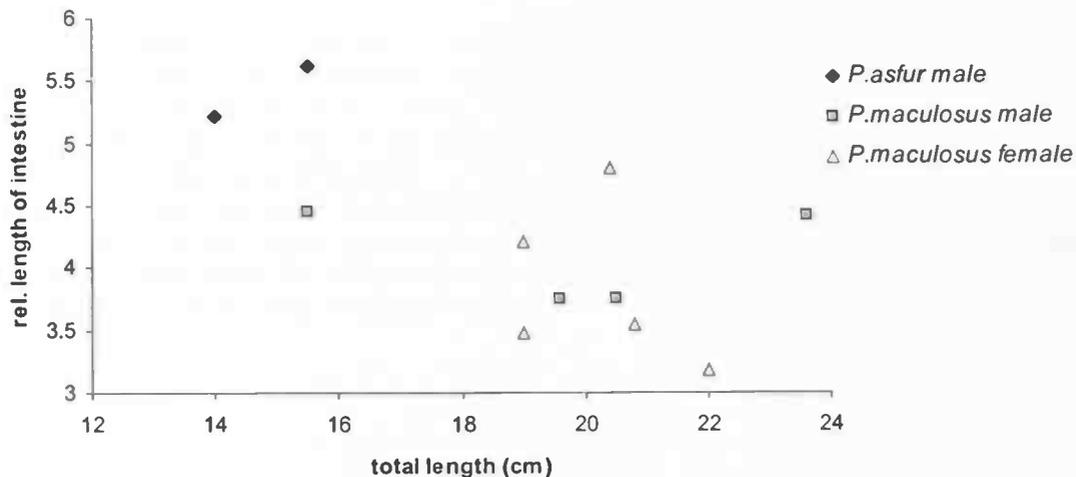


Figure 8: Relative length of the intestine versus total body length for the dissected individuals of *P.asfur* and *P.maculosus*.

Stomach contents

The stomach and terminal sac were both fully packed in every individual. Remarkable was that the particle size and the consistency of the stomach contents differed between the two angelfish species. The stomach contents of *P.maculosus* were quite dry and clotted in packages. The material was firm and compressed. On the contrary, the stomach contents of *P.asfur* were loose and dissolved in stomach fluid. They formed pulverised, fine material.

Table 1 gives the food-items that were found in the stomach content samples of every dissected individual in percentages.

Table 1: Stomach content of each individual of P.asfur and P.maculosus, given in percentages.

| Category | Food item | mac1 | mac2 | mac3 | mac4 | mac5 | mac6 | asf1 | asf2 | MAC | std | ASF | std | | |
|---------------------|---------------------------------|------|------|------|------|------|------|------|------|------|------|-------------|------|------|-------------|
| <u>Sponges</u> | sponges | 20 | 20.5 | 27.5 | 26 | 17 | 26 | 19.5 | 27.5 | 22.8 | 4.23 | <u>22.8</u> | 23.5 | 5.66 | <u>23.5</u> |
| <u>Green Algae</u> | <i>Enteromorpha</i> | 0 | 2 | 2 | 2 | 1 | 0 | 4.5 | 3.5 | 1.2 | 0.98 | <u>2.8</u> | 4.0 | 0.71 | <u>4.5</u> |
| | <i>Cladophora</i> | 2 | 2 | 1.5 | 0 | 3 | 1 | 0 | 1 | 1.6 | 1.02 | | 0.5 | 0.71 | |
| <u>Brown Algae</u> | <i>Turbinaria</i> | 20.5 | 14 | 16.5 | 14.5 | 20.5 | 9.5 | 11 | 13 | 15.9 | 4.22 | <u>15.9</u> | 12.0 | 1.41 | <u>12</u> |
| <u>Red Algae</u> | <i>Hypnea</i> | 11 | 15.5 | 11.5 | 5.5 | 11 | 8 | 10 | 9 | 10.4 | 3.40 | <u>33.2</u> | 9.5 | 0.71 | <u>32.0</u> |
| | <i>cervicornis</i> | | | | | | | | | | | | | | |
| | <i>Hypnea musciformis</i> | 7.5 | 4 | 4.5 | 2.5 | 4 | 4.5 | 4.5 | 5.5 | 4.5 | 1.64 | | 5.0 | 0.71 | |
| | <i>Pterocladia cearulescens</i> | 8 | 11.5 | 14 | 16 | 8 | 5 | 13 | 9.5 | 10.4 | 4.15 | | 11.3 | 2.47 | |
| | <i>Gelidiopsis inticata</i> | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0.8 | 0.98 | | 0.0 | 0.00 | |
| | <i>Gelidiella myriocladi</i> | 3 | 3 | 1 | 1 | 3.5 | 4 | 3.5 | 1 | 2.6 | 1.28 | | 2.3 | 1.77 | |
| | <i>Gelidium</i> | 2.5 | 8.5 | 3.5 | 3.5 | 7 | 1.5 | 3 | 5 | 4.4 | 2.73 | | 4.0 | 1.41 | |
| <u>Unidentified</u> | unidentified | 20.5 | 16 | 17 | 18.5 | 18 | 30 | 27 | 21.5 | 20.0 | 5.13 | <u>20</u> | 24.3 | 3.89 | <u>24.3</u> |
| <u>Other</u> | unidentified | 6 | 1 | 1 | 2.5 | 1 | 5.5 | 2.5 | 2.5 | 2.8 | 2.34 | <u>7.2</u> | 2.5 | 0.00 | <u>4.3</u> |
| | algae | | | | | | | | | | | | | | |
| | coral | 1.5 | 1.5 | 1 | 2 | 2.5 | 0 | 0 | 0 | 1.4 | 0.86 | | 0.0 | 0.00 | |
| | tunicates | 1 | 1 | 0 | 6.5 | 1 | 5 | 1.5 | 1 | 2.4 | 2.65 | | 1.3 | 0.35 | |
| | shell | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0.5 | 1.22 | | 0.0 | 0.00 | |
| | fish | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.0 | 0.00 | | 0.5 | 0.71 | |

The diet of *P.asfur* and *P.maculosus* mainly consists of Sponges and Red Algae (mainly *Hypnea cervicornis* and *Pterocladia cearulescens*). Brown Algae (all *Turbinaria*), Green Algae and Other (coral, tunicates, shell, fish and unidentified algae) were present in a less amount. On average, one fifth of the stomach contents appeared to be unrecognisable and was part of the category Unidentified.

Table 6 (see appendix 6) shows that almost every food item participates in the diet of all individuals. The red algae *Gelidiopsis inticata*, both green algae and the entire category Other are the exceptions, but it must be mentioned that all these food items are not common and that they contribute very little to the total diet.

Looking at the graph that shows the stomach contents divided into categories for every individual, there seems to be a great variation between individuals. After analysing the data with a Single Factor ANOVA, the stomach contents appear not to differ between individuals of both species ($p = 0.999$; $\alpha = 0.05$).

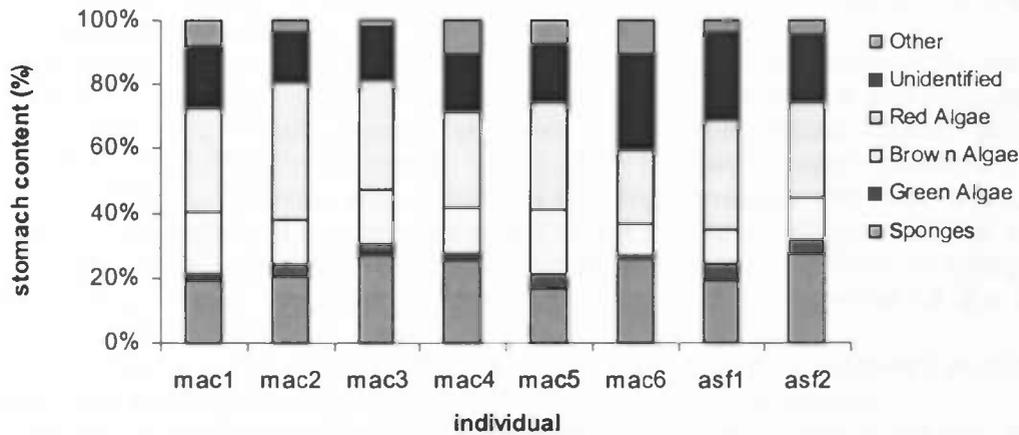


Figure 9: Categorized stomach contents of all individuals for *P.asfur* and *P.maculosus*.

When comparing gender and species, there are no differences in diet composition (Single Factor ANOVA: $p = 0.999$; $\alpha = 0.05$) (see figure 10).

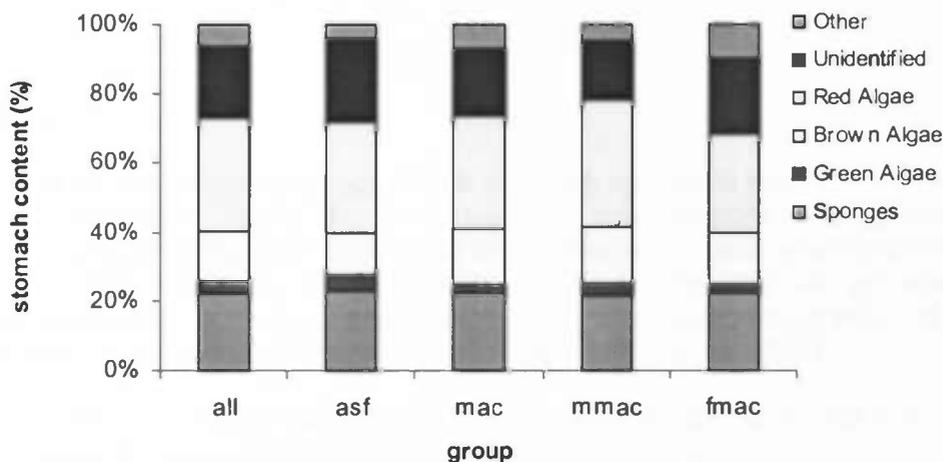


Figure 10: Categorized stomach contents grouped by species and gender for *P.asfur* ($n=2$) and *P.maculosus* (males: $n=4$; females: $n=5$).

The intestines and terminal sacs roughly contained the same food items as the stomachs, but the amount that was recognisable was much smaller. In every individual, only a few species were present and identifiable (see appendix 5).

It is notable that besides the food items like in the stomach, these parts of the digestive tract contain a reasonable amount of undigested, solid material, such as pieces of corals and complete shells.

Discussion

Feeding activity

Looking at the entire day, the bite rate of *P.asfur* is higher than the bite rate of *P.maculosus*. The bite rates of the individuals of both species vary to a great extent. Therefore, it cannot be said whether the species as a group show variation in feeding activity during the day or if they feed at a constant rate.

These results would be in contrast with earlier research on foraging periodicity, which states that a peak in feeding activity occurs in the afternoon for tropical and temperate blennioid fish, Caribbean and Pacific damselfish, and some West Indian Ocean surgeon fish (Montgomery, 1980; Polunin & Klumpp, 1989). More detailed research performed by Zoufal & Taborsky (1991) on blenniids shows that fish foraging correlates with daily changes of diet quality; the energy content in algae increases in the afternoon. Bruggemann *et al.* (1994a) state in their article about food intake of parrotfish that this increase in energy can be explained by a rise in the organic fraction (AFDM) and an increase of the potentially digestible soluble carbohydrate content.

It has to be mentioned though, that these fish were all considered herbivorous, in contrast to the investigated angelfish, which appeared to be omnivorous. Research has to be performed on the preference for food items during the day. It might be that these omnivorous angelfish eat a high amount of algae in the afternoon, and change to sponges, corals and other small animals in the morning and in the evening.

Another thing that Bruggemann (1994a) has discovered in his research on parrotfish is that bigger fish take bigger bites, with the consequence that the bite rate of big fish is lower than the bite rate of smaller fish. In this project on angelfish, this cannot be concluded.

For the individuals of *P.asfur* there is a huge variation in average bite rate for every individual at approximately the same body length. The individuals of the species *P.maculosus* hardly differ in average bite rate at a larger size range. Bite rate is not correlated to the size of the fish.

Dissections

The structure of the digestive tract of both angelfish species is similar. According to Lobel (1981), the presence of a long intestine and terminal sac can be explained by classifying both species as omnivores, with some preadaptations to herbivory. A long intestine increases the absorption area and a terminal sac provides the ability of having symbiotic micro-organisms, which may help with degradation of cellulose and structurally similar compounds (Rimmer & Wiebe, 1987; Horn, 1989).

The only difference found between these two angelfish species is that the relative intestine length in relation to the total body length is bigger for *P.asfur*.

P.asfur might have a higher capacity for nutrient absorption since its intestine is relatively larger than that of *P.maculosus*.

Stomach contents

The stomach contents of the two angelfish species differ in particle size and consistency. The stomach contents of *P.asfur* were very fine in structure, whereas in *P.maculosus* the contents were clotted in packages. This also indicates a higher capacity for nutrient absorption in *P.asfur*.

The fact that the stomach content of *P.maculosus* consists of coarse material clotted in packages and the stomach content of *P.asfur* contains pulverised, fine material, might be related to differences in bite rate. *P.asfur* has a higher bite rate and considering the presence of fine material in stomach contents, this species might take smaller bites. This can be easily checked by performing research in the field on the difference in bite size, so this is highly recommended.

P.asfur and *P.maculosus* are basically omnivorous, mainly feeding on sponges and algae, but solid material like coral and shell is also eaten. Almost every recognised food-item, at least all common ones, turned out to be part of the diet of all individuals.

There appeared to be no differences in diet composition between individuals, species and gender.

The dietary overlap of these angelfish species is high, but this does not necessarily mean that the species are competing. Hourigan *et al.* (1989) found that food was not a limiting resource for three other species of the family of pomacanthids in the Caribbean, even though the three species were cohabitants.

P.asfur and *P.maculosus* are omnivorous and have a broad range of food items at their disposal. This wide range of diet reduces intraspecific competition and may also reduce interspecific competition, according to Pérez-España & Abitia-Cárdenas (1996). Furthermore, *P.asfur* is smaller than *P.maculosus* and is therefore able to forage on other places, for example in caves.

Research on feeding data by the classic method of stomach content analysis alone is not sufficient. Part of the stomach content might already be digested and will therefore not be recognised. For further research it is therefore recommended to observe the bites of the fish in the field and use those in addition to determine diet composition.

Some diet components might still not contribute to the metabolism of the fish, because they are only digested partly, or not at all. It is possible to investigate this aspect by looking at digestive mechanisms such as microbial fermentation, which probably occurs in the terminal sac. The microbiota produce short-chain fatty acids (SCFAs) and these can be biochemically analysed to determine the dietary resources (Clements & Choats, 1995). This method will also provide sustained information about the method of digestion by the fish; a low level of SCFAs indicates the use of other mechanisms for trituration of ingested material, such as acid lysis in a thin walled stomach, pulverisation in a muscular stomach or trituration in pharyngeal jaws (Horn, 1989).

Conclusions

It is not clear whether the feeding activity in terms of bite rate of *Pomacanthus asfur* and *P.maculosus* varies during the day. Looking at the entire day, *P.asfur* appears to have a higher bite rate than *P.maculosus*.

Both species turn out to have the same structure of digestive tract and the same diet composition based on stomach contents; both angelfish are generalist omnivores with adaptations to herbivory. The feeding habit is reflected in the structure of their digestive tract by the relative strong stomach, long intestine and terminal sac.

P.asfur has a relative longer intestine than *P.maculosus* and together with the fact that its stomach contents are already more pulverised, it seems to have a higher capacity for nutrient absorption than *P.maculosus*.

It is important to keep in mind that all conclusions are based on a small number of observed and dissected fish. Large scale studies are necessary to determine the feeding ecology in detail.

Still, we managed to make a good setup, which can form a fundamental basis for further research on these angelfish species.

References

- * Baldwin, M.F.; 1991; Natural resources of Sri Lanka, conditions and trends; *The Natural Resources, Energy and Science Authority of Sri Lanka (NARESA)*.
- * Bakus, G.J.; 1966; Some relationships of fishes to benthic organisms on coral reefs; *Nature*; Vol. 210: p. 280-284.
- * Bruggemann, J.H., Begeman, J., Bosma, E.M., Verburg, P., Breeman, A.M.; 1994a; Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein, and energy; *Marine Ecology Program Series*; Vol. 112: p. 51-66.
- * Clements, K.D., Choat, J.H.; 1995; Fermentation in tropical marine herbivorous fishes; *Physiological Zoölogy*; Vol. 68: p. 355-378.
- * Debelius, H.; 1993; Indian Ocean – Tropical fish guide; *IKAN – Unterwasser Archiv*.
- * Doherty, P.J. & Williams, D.McB.; 1988; The replenishment of coral reef fish populations; *Oceanography and Marine Biology*; Vol. 26: p. 487-551.
- * Fraser-Brunner, A.; 1933; A revision of chaetodont fishes of the subfamily Pomacanthinae; *Proceedings of the Zoological Society of London*; p. 543-599.
- * Haydar, D.; 1998; Heavenly creatures: Behaviour, population structure and abundance of the angelfish species *Pomacanthus asfur* and *Pomacanthus maculosus*; *Report of a MSc-project, department of Marine Biology, University of Groningen*.
- * Horn, M.H.; 1989; Biology of marine herbivorous fishes; *Oceanographic Marine Biology Annual Review*; Vol. 27: p. 167-263.
- * Hourigan, T.F., Stanton, F.G., Motta, P.J., Kelley, C.D. & Carlson, B.; 1989; The feeding ecology of three species of Caribbean angelfishes (Family Pomacanthidae); *Environmental Biology of Fishes*; Vol. 24: p. 105-116.
- * Howe, J.C.; 1993; A comparative analysis of the feeding apparatus in pomacanthids, with special emphasis of oesophageal papillae in *Genicanthus personatus*; *Journal of Fish Biology*; Vol. 43: p. 593-602.
- * Hughes, T.P.; 1994; Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef; *Science*; Vol. 265: p. 1547-1551.
- * Jennings, S. & Lock, J.M.; 1996; Population and ecosystem effects of fishing; *In: Reef Fisheries, Polunin, N.V.C. and Roberts, C.M.; Chapman and Hall, London*; p. 193-218.
- * Jennings, S. & Polunin, N.V.C.; 1996; Impacts of fishing on tropical reef ecosystems; *Ambio*; Vol. 25 (1): p. 44-49
- * Jones, R.S.; 1968; A suggested method for quantifying gut contents in herbivorous fishes; *Micronesia*; Vol. 4: p. 369-371.
- * Lobel, P.S.; 1981; Trophic biology of herbivorous reef fishes: alimentary, pH, and digestive capabilities; *Journal of Fish Biology*; Vol. 19: p. 365-397.

- * Montgomery, W.L.; 1980; Comparative feeding ecology of two herbivorous damselfishes (Pomacentridae: Teleostei) from the gulf of California, Mexico; *Journal of Experimental Marine Biology and Ecology*; Vol. 47: p. 9-24.
- * Öhman, M.C. & Rajasuriya, A. & Lindén, O.; 1993; Human Disturbances on coral reefs in Sri Lanka: A case study; *Ambio*; Vol. 22 (7): p. 474-480.
- * Pérez- España, H. & Abitia-Cárdenas, L. A.; 1996; Description of the digestive tract and feeding habits of the king angelfish and the Cortes angelfish; *Journal of Fish Biology*; Vol. 48:p. 807-817.
- * Polunin, N.V.C. & Klumpp, D.W.; 1989; Ecological correlates of foraging periodicity in herbivorous reef fish of the Coral Sea; *Journal of Experimental Marine Biology and Ecology*; Vol. 126: p. 1-20.
- * Randall, J.E.; 1983; Red Sea Reef Fishes; *Immel Publishing Limited, London*.
- * Randall, J.E. & Yasuda, J.; 1979; *Centropyge shepardi*, a new angelfish from the Mariana and Ogasawara Islands; *Japanese Journal of Ichthyology*; Vol. 26: p. 55-61.
- * Reynolds, W. W. & Reynolds, L.J.; 1976; Observations on food habits of the angelfishes *Pomacanthus zonipectus* and *Holacanthus passer* in the Gulf of California; *California Fish and Game*; Vol. 63: p. 124-125.
- * Rimmer, D.W. & Wiebe, W.J.; 1987; Fermentative microbial digestion in herbivorous fishes; *Journal of fish Biology*; Vol. 31: p. 229-236.
- * Russ, G.R.; 1991; Coral reef fisheries: effects and yields. In: *The Ecology of fishes on coral reefs*; Sale, P.F.; *Academic Press, San Diego*; p. 601-635.
- * Sakai, Y. & Kohda, M.; 1995; Foraging by mixed-species groups involving a small angelfish, *Centropyge ferrugates* (Pomacanthidae); *Journal of Ichthyological Research*; Vol. 41 (4): p. 429-435.
- * Smith, M.M. & Heemstra, P.C.; 1986; Smiths' sea fishes; *Springer*, p. 623-626.
- * Thresher, R.E.; "Reproduction in reef fishes"; *TFH Publishers, Neptune City*, p. 244-261.
- * Weatherley, A.H. & Gill, H.S.; 1987; The biology of fish growth; *Academic Press Inc., London*; p. 14-20.
- * Williams, D.M.; 1991; Patterns and processes in the distribution of coral reef fishes; In: *The ecology of fishes on coral reefs*; Sale, P.F.; *Academic press, San Diego*; p.437-474.
- * Wootton, R.J.; 1985; Energetics of reproduction; In: *Fish energetics: new perspectives*; Tyler, P. & Calow, P.; *Croom Helm, London*; p. 231-254.
- * Zoufal, R. & Taborsky, M.; 1991; Fish foraging periodicity correlates with daily changes of diet quality; *Marine Biology*; Vol. 108 (2): p. 193-196.

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Appendix

Appendix 1: List of all fish recorded on the study site in front of the fieldstation from the department of Marine Biology and Fisheries of the University of Asmara (Februari – Juni 1998).

| | | | |
|--------------------------------------|--------------------------|-----------------------------------|---------------------------------|
| <i>Abudefduf sexfasciatus</i> | Scissortail Sergeant | <i>Neopomacentrus xanthurus</i> | Yellowtail Damselfish |
| <i>Abudefduf saxatilis</i> | Sergeant Major | <i>Ostracion cyanurus</i> | Cube Trunkfish |
| <i>Acanthopagrus bifasciatus</i> | Doublebar Bream | <i>Paraglyphidodon melas</i> | Royal Damselfish |
| <i>Acanthurus nigricans</i> | Black Surgeonfish | <i>Pardachirus marmoratus</i> | Moses' Sole |
| <i>Acanthurus nigrofocous</i> | Brown Surgeonfish | <i>Parupeneus forsskali</i> | Forsskal's Goatfish |
| <i>Acanthurus sohal</i> | Sohal | <i>Platax orbicularis</i> | Circular Batfish |
| <i>Adioryx ruber</i> | Redcoat | <i>Plectorhinchus gaterinus</i> | Blackspotted Sweetlips |
| <i>Amblyglyphidodon flavilatus</i> | Yellowflank Damselfish | <i>Plectrogyphidon lacrymatus</i> | Jewel Damselfish |
| <i>Amphiprion bicinctus</i> | Two-bar Anemonefish | <i>Plotosus lineatus</i> | Striped Eel Catfish |
| <i>Apogon bifasciatus</i> | Doublebar Cardinalfish | <i>Pomacanthus asfur</i> | Arabian Angelfish |
| <i>Arothron diadematus</i> | Masked Puffer | <i>Pomacanthus maculosus</i> | Yellowbar Angelfish |
| <i>Caesio striatus</i> | Striated Fusilier | <i>Pomacentrus trichourus</i> | Reticulated Damselfish |
| <i>Carangoides bajad</i> | Orangespotted Trevally | <i>Pomacentrus trilineatus</i> | Threeline Damselfish |
| <i>Carangoides fulvoguttatus</i> | Yellowspotted Jack | <i>Pseudobalistes fuscus</i> | Blue Triggerfish |
| <i>Caranx melampygus</i> | Bluefin Trevally | <i>Pseudochromis flavivertex</i> | Sunrise Dottyback |
| <i>Cephalopholis hemistiktos</i> | Halfspotted Grouper | <i>Pseudochromis sankeyi</i> | Striped Dottyback |
| <i>Chaetodon auriga</i> | Threadfin Butterflyfish | <i>Pseudochromis springeri</i> | Bluestriped Dottyback |
| <i>Chaetodon fasciatus</i> | Striped Butterflyfish | <i>Pterocaesio chrysozona</i> | Goldband Fusilier |
| <i>Chaetodon mesoleucos</i> | Paleface Butterflyfish | <i>Rhabdosargus sarba</i> | Yellowfin Bream |
| <i>Chaetodon semilarvatus</i> | Masked Butterflyfish | <i>Scarus ferrugineus</i> | Rusty Parrotfish |
| <i>Chromis caerulea</i> | Bluegreen Chromis | <i>Scarus psittacus</i> | Palenose Parrotfish |
| <i>Chrysiptera unimaculata</i> | Onespot Damselfish | <i>Scarus sordidus</i> | Bullethead Parrotfish |
| <i>Coris aygula</i> | Clown Coris | <i>Scolopsis ghanan</i> | Dotted Spinecheek |
| <i>Corythoichthys flavofasciatus</i> | Network Pipefish | <i>Sphyaena barracuda</i> | Great Barracuda |
| <i>Ctenochaetus striatus</i> | Lined Bristletooth | <i>Sidera Grisea</i> | Grey Moray |
| <i>Ctenogobiops feroculus</i> | Spotted Partnerygoby | <i>Siganus stellatus</i> | Brown-spotted Rabbitfish |
| <i>Dascyllus marginatus</i> | Blackbordered Dascyllus | <i>Sufflamen albicaudatus</i> | Bluethroat Triggerfish |
| <i>Dascyllus trilineatus</i> | Three-spot Dascyllus | <i>Taeniura lymma</i> | Bluespotted Reef Stingray |
| <i>Diplodus noct</i> | Arabian Pinfish | <i>Thalassoma lunare</i> | Moon Wrasse |
| <i>Echeneis naucrates</i> | Striped Remora | <i>Thalassoma purpureum</i> | Surge Wrasse |
| <i>Epinephelus malabaricus</i> | Malabar Grouper | <i>Trachinotus blochii</i> | Bloch's Pompano |
| <i>Epinephelus summana</i> | Summana Grouper | <i>Variola louti</i> | Lunartail grouper |
| <i>Ecsenius aroni</i> | Aron's blenny | <i>Zembrasoma desjardinii</i> | Indian Sailfin Tang |
| <i>Fistularia commersomii</i> | Cornetfish | <i>Zembrasoma xanthurum</i> | Yellowtail Surgeonfish |
| <i>Gnathadon speciosus</i> | Golden Pilot Jack | | |
| <i>Gonochaetodon larvatus</i> | Orangeface Butterflyfish | | (Randall, 1983; Debelius, 1993) |
| <i>Halichoeres hortulanus</i> | Checkerboard wrasse | | |
| <i>Halichoeres scapularis</i> | Zigzag Wrasse | | |
| <i>Hemigymnus fasciatus</i> | Barred Wrasse | | |
| <i>Hemiramphus far</i> | Spotted Halfbeak | | |
| <i>Heniochus diphreutes</i> | Pennantfish | | |
| <i>Heniochus intermedius</i> | Red Sea Bannerfish | | |
| <i>Himantura uarnak</i> | Honeycomb Stingray | | |
| <i>Hipposcarus harid</i> | Longnose Parrotfish | | |
| <i>Hyporhamphus gambarur</i> | Red Sea Halfbeak | | |
| <i>Labroides dimidiatus</i> | Cleaner Wrasse | | |
| <i>Larabicus quadrilineatus</i> | Fourline Wrasse | | |
| <i>Lethrinus mahsena</i> | Mashena Emperor | | |
| <i>Lethrinus nebulosus</i> | Bluescaled Emperor | | |
| <i>Lotilia graciliosa</i> | Whitecap Partnerygoby | | |
| <i>Lutjanus argentimaculatus</i> | River Snapper | | |
| <i>Lutjanus ehrenbergi</i> | Blackspot Snapper | | |
| <i>Lutjanus monostigma</i> | Onespot Snapper | | |
| <i>Myripristis xanthacrus</i> | Yellowtip Soldierfish | | |

Appendix 2: Intraspecific variation in number of bites/hour at different parts of the day for *P.asfur* and *P.maculosus*.

Figure 4 shows that the bite rates during different parts of the day differ greatly among individual fish. There is a high intraspecific variation for both species during several parts of the day as shown by the p-values of the Single Factor ANOVA. Therefore, comparison between parts of the day is not possible.

*Table 2: P-values for intraspecific variation in number of bites per hour at different parts of the day for *P.asfur* and *P.maculosus*.*

| <i>Part of the day</i> | <i>P.asfur</i> | <i>P.maculosus</i> |
|------------------------|----------------|--------------------|
| 7.00 – 10.00 h. | 0.018 (n=3) | 0.103 (n=5) |
| 10.00 - 13.00 h. | 0.044 (n=6) | 0.848 (n=7) |
| 13.00 - 16.00 h. | 0.312 (n=6) | 0.897 (n=6) |
| 16.00 – 19.00 h. | 0.002 (n=5) | 0.014 (n=7) |

Appendix 3: Dissection

Table 3: Rough data of all dissected fish.

| IND | length (cm) | | body depth | | length of digestive tract (cm) | | | bodyweight empty (g) | | | relation |
|-------|-------------|-------|------------|-------|--------------------------------|-----------|----------|----------------------|------|-------|----------|
| | standard | total | (cm) | depth | stomach | intestine | term.sac | total | wet | dry | |
| asf1 | 11.5 | 14 | 8.5 | 6 | 73 | 6 | 85 | 77.9 | 25.9 | 0.332 | |
| asf2 | 12.5 | 15.5 | 11 | 6 | 87 | 5 | 98 | 114.1 | 42.9 | 0.376 | |
| macm1 | 12 | 15.5 | 9 | 6 | 69 | 5 | 80 | 99.4 | 32.3 | 0.325 | |
| macm2 | 15.5 | 19.6 | 12.5 | 7.4 | 73.4 | 6.8 | 87.6 | 212.8 | 68.8 | 0.323 | |
| macm3 | 16.5 | 20.5 | 10.5 | 7 | 77 | 6.5 | 90.5 | 194.2 | 66.7 | 0.344 | |
| macm4 | 17.7 | 23.6 | 12.4 | 9.7 | 104.4 | 7.2 | 121.3 | 293.5 | 95.2 | 0.324 | |
| macf1 | 14.8 | 19 | 11 | 7.4 | 66.2 | 5.9 | 79.5 | 186.1 | 56.0 | 0.301 | |
| macf2 | 15 | 19 | 12 | 8 | 80 | 9.5 | 97.5 | 164.5 | 50.7 | 0.308 | |
| macf3 | 15.6 | 20.4 | 10.9 | 7 | 98 | 6.2 | 111.2 | 223.4 | 76.9 | 0.344 | |
| macf4 | 15.9 | 20.8 | 12 | 7.4 | 73.6 | 9.7 | 90.7 | 211.8 | 69.1 | 0.326 | |
| macf5 | 18 | 22 | 12.5 | 8.5 | 70 | 10 | 88.5 | 232.3 | 81.2 | 0.350 | |

| IND. | weight of full dig. tract (g) | | | | weight of empty digestive tract (g) | | | | weight of content | | | | | | | |
|-------|-------------------------------|------|------|------|-------------------------------------|-----|-------|-----|-------------------|-----|------|-----|-------|-----|-------|------|
| | stom. | | int. | | term. | | total | | stom. | | int. | | term. | | total | |
| | wet | dry | wet | dry | wet | dry | wet | dry | wet | dry | wet | dry | wet | dry | wet | dry |
| asf1 | 3.1 | 2.7 | 3.4 | 12 | 1.4 | 0.4 | 0.6 | 0.2 | 0.4 | 0.1 | 2.4 | 0.7 | 1.7 | 2.1 | 3 | 5.1 |
| asf2 | 3.7 | 2.8 | 3.8 | 15.3 | 2.1 | 0.5 | 0.8 | 0.3 | 0.5 | 0.1 | 3.4 | 0.9 | 1.6 | 2 | 3.3 | 6.9 |
| macm1 | 3.2 | 4.7 | 5.1 | 15.5 | 1.1 | 0.3 | 1.7 | 0.4 | 0.6 | 0.1 | 3.4 | 0.8 | 2.1 | 3 | 4.5 | 9.6 |
| macm2 | 7.2 | 11.7 | 10.7 | 37.9 | 2.7 | 0.6 | 3.5 | 1 | 1.2 | 0.3 | 7.4 | 1.9 | 4.5 | 8.2 | 9.5 | 22.2 |
| macm3 | 6.5 | 6.1 | 11 | 29.9 | 2.8 | 0.6 | 3.8 | 1.4 | 1.2 | 0.3 | 7.8 | 2.3 | 3.7 | 2.3 | 9.8 | 15.8 |
| macm4 | 9.5 | 13 | 14.8 | 47.1 | 3.8 | 0.7 | 3.7 | 0.9 | 1.3 | 0.2 | 8.8 | 1.8 | 5.7 | 9.3 | 13.5 | 28.5 |
| macf1 | 5 | 8.7 | 13.4 | 33.8 | 2.3 | 0.5 | 2.7 | 0.6 | 1.2 | 0.2 | 6.2 | 1.3 | 2.7 | 6 | 12.2 | 20.9 |
| macf2 | 5 | 4.5 | 12.3 | 24.9 | 2.1 | 0.4 | 2.3 | 0.5 | 0.9 | 0.2 | 5.3 | 1.1 | 2.9 | 2.2 | 11.4 | 16.5 |
| macf3 | 6.5 | 8.9 | 9.8 | 35.2 | 3 | 0.6 | 2.8 | 1.2 | 1.8 | 0.4 | 7.6 | 2.2 | 3.5 | 6.1 | 8 | 17.6 |
| macf4 | 5.3 | 8.5 | 14.2 | 34.8 | 2.5 | 0.5 | 3.1 | 1 | 1.2 | 0.3 | 6.8 | 1.8 | 2.8 | 5.4 | 13 | 21.2 |
| macf5 | 10.5 | 13 | 7.7 | 41 | 5.8 | 1.5 | 3.9 | 1.2 | 1.8 | 0.4 | 12 | 3.1 | 4.7 | 9.1 | 5.9 | 19.7 |

| IND. | weight (g) | | | | somatic indexes | | | | | |
|-------|------------|-----|--------|-----|-----------------|-----|-------|-------|--------|-----|
| | liver | | gonads | | fat | | liver | | gonads | fat |
| | wet | dry | wet | dry | wet | dry | LSI | GSI | FSI | |
| asf1 | 0.8 | 0.2 | 0.1 | 0 | 1.3 | 1 | 1.027 | 0.064 | 1.669 | |
| asf2 | 1.1 | 0.3 | 0.2 | 0 | 3.6 | 2.7 | 0.964 | 0.175 | 3.155 | |
| macm1 | 1.1 | 0.3 | 0.1 | 0 | 0.3 | 0.2 | 1.107 | 0.050 | 0.302 | |
| macm2 | 2.5 | 0.7 | 0.1 | 0 | 0.3 | 0.2 | 1.175 | 0.047 | 0.141 | |
| macm3 | 2.5 | 0.6 | 0.1 | 0 | 0.9 | 0.8 | 1.287 | 0.051 | 0.463 | |
| macm4 | 4.6 | 1.2 | 0.2 | 0 | 2.5 | 1.2 | 1.567 | 0.068 | 0.852 | |
| macf1 | 2.2 | 0.5 | 0.4 | 0.1 | 0.1 | 0.1 | 1.182 | 0.215 | 0.054 | |
| macf2 | 2.3 | 0.6 | 0.1 | 0 | 0 | 0 | 1.398 | 0.061 | 0.012 | |
| macf3 | 2.3 | 0.6 | 0.5 | 0.1 | 2.9 | 2 | 1.030 | 0.224 | 1.298 | |
| macf4 | 2.7 | 0.7 | 0.4 | 0.1 | 0.9 | 0.5 | 1.275 | 0.189 | 0.425 | |
| macf5 | 3.4 | 0.9 | 0.6 | 0.1 | 2 | 1.1 | 1.464 | 0.258 | 0.861 | |

Appendix 4: Results of the analysis of data on digestive tract and its contents.

The length of each digestive tract and its separate parts (stomach, intestine and terminal sac) was compared with the total length of the fish.

The wet weights of each digestive tract and its three separate parts were plotted against the wet body weight of the fish.

For every comparison a linear relationship is expected according to $y = mx + b$ (x = length of (part of) digestive tract in cm, or wet weight of content of (part of) digestive tract in g; y = total body length in cm, or wet body weight in g.).

The linear regression coefficient is given. *P.asfur* has only got a sample size of 2, and will therefore show a perfect linear regression for every comparison made. The data set for *P.asfur* is thus too small to yield valid results.

P.maculosus has a sample size of 9, and therefore the regression coefficient should be higher than 0.666 to show a significant relation.

Table 4: Comparisons of the data on digestive tract and the body for P.asfur and P.maculosus.

| Comparison between: | <i>P.asfur</i> | | | | <i>P.maculosus</i> | | | |
|--|----------------|----------|----------|----------|--------------------|----------|----------|----------|
| | m | b | r | n | m | b | r | n |
| Length digestive tract and total body length | 8.667 | 85 | 1 | 2 | 4.116 | 175.4 | 0.664 | 9 |
| Length stomach and total body length | 0 | 6 | x | 2 | 0.390 | 5.830 | 0.836 | 9 |
| Length intestine and total body length | 8.667 | 85 | 1 | 2 | 3.335 | 63.91 | 0.563 | 9 |
| Length terminal sac and total body length | -0.67 | 6 | 1 | 2 | 0.392 | 5.643 | 0.478 | 9 |
| Wet weight content digestive tract and wet body weight | 21.11 | 83 | 1 | 2 | 9.153 | 62.21 | 0.556 | 9 |
| Wet weight content stomach and wet body weight | -380 | 83 | -1 | 2 | 55.4 | 64.93 | 0.746 | 9 |
| Wet weight intestine and total body length | -380 | 83 | -1 | 2 | 11.16 | 118.8 | 0.364 | 9 |
| Wet weight terminal sac and total body length | 126.7 | 83 | 1 | 2 | 8.808 | 103 | 0.323 | 9 |

Appendix 5: Contents of the digestive tract.

Table 5: Original stomach contents grouped by species and gender given in percentages.

| CATEGORY | FOOD ITEM | all | asf | mac | macm | macf | average |
|-------------|---------------------------------|------|------|------|------|------|---------|
| Sponges | Sponges | 23.0 | 23.5 | 22.8 | 22.7 | 23.0 | 23.0 |
| Green Algae | <i>Enteromorpha</i> | 1.9 | 4.0 | 1.2 | 1.3 | 1.0 | 1.9 |
| | <i>Cladophora</i> | 1.5 | 0.5 | 1.9 | 1.8 | 2.0 | 1.5 |
| Brown Algae | <i>Turbinaria</i> | 14.9 | 12.0 | 15.9 | 17.0 | 14.8 | 14.9 |
| Red Algae | <i>Hypnea cervicornis</i> | 10.2 | 9.5 | 10.4 | 12.7 | 8.2 | 10.2 |
| | <i>Hypnea musciformis</i> | 4.6 | 5.0 | 4.5 | 5.3 | 3.7 | 4.6 |
| | <i>Pterocladia cearulescens</i> | 10.6 | 11.3 | 10.4 | 11.2 | 9.7 | 10.6 |
| | <i>Gelidiopsis inticata</i> | 0.6 | 0.0 | 0.8 | 1.0 | 0.7 | 0.6 |
| | <i>Gelidiella myriocladi</i> | 2.5 | 2.3 | 2.6 | 2.3 | 2.8 | 2.5 |
| | <i>Gelidium</i> | 4.3 | 4.0 | 4.4 | 4.8 | 4.0 | 4.3 |
| Rubbish | Rubbish | 21.1 | 24.3 | 20.0 | 17.8 | 22.2 | 21.1 |
| Other | Unidentified | 2.8 | 2.5 | 2.8 | 2.7 | 3.0 | 2.8 |
| | Coral | 1.1 | 0.0 | 1.4 | 1.3 | 1.5 | 1.1 |
| | Tunicates | 2.1 | 1.3 | 2.4 | 0.7 | 4.2 | 2.1 |
| | Shell | 0.4 | 0.0 | 0.5 | 0.0 | 1.0 | 0.4 |
| | Fish | 0.1 | 0.5 | 0.0 | 0.0 | 0.0 | 0.1 |

Content of intestine:

- mac1: Sponges, *Cladophora*, *Turbinaria*, *Pterocladia cearulescens*, *Gelidiella myriocladi* and coral
 mac2: Sponges, *Turbinaria*, *Hypnea cervicornis*, *Hypnea musciformis*, *Pterocladia cearulescens*, and aluminiumfoil
 mac3: Sponges, *Turbinaria*, *Pterocladia cearulescens*, and transparent "skeleton"
 mac4: Sponges, *Hypnea cervicornis*, *Hypnea musciformis*, unidentified algae, coral, pieces of bones and two worms
 asf1: Sponges, *Turbinaria*, *Pterocladia cearulescens*, unidentified, coral, tunicates, pieces of bones and transparent "skeleton"
 asf2: Sponges and pieces of bones

Content of terminal sac:

- mac1: Sponges, *Turbinaria*, *Hypnea cervicornis*, *Gelidiopsis inticata*, unidentified algae, snails
 mac2: Sponges, *Turbinaria*, *Hypnea cervicornis*, lots of corals, slug, bivalves, shells
 asf1: Sponges, *Turbinaria*, *Hypnea cervicornis*, *Gelidium*

Appendix 6: Presence of food items given in percentages for both species.

Table 6: Percentage of food items present in the diet of individuals for *P.asfur* (n=2) and *P.maculosus* (n=6).

| CATEGORY | FOOD ITEM | percentage of fish containing each item |
|-------------|---------------------------------|---|
| Sponges | sponges | 100 |
| Green Algae | <i>Enteromorpha</i> | 78 |
| | <i>Cladophora</i> | 78 |
| Brown Algae | <i>Turbinaria</i> | 100 |
| Red Algae | <i>Hypnea cervicornis</i> | 100 |
| | <i>Hypnea musciformis</i> | 100 |
| | <i>Pterocladia cearulescens</i> | 100 |
| | <i>Gelidiopsis inticata</i> | 33 |
| | <i>Gelidiella myriocladi</i> | 100 |
| | <i>Gelidium</i> | 100 |
| Rubbish | rubbish | 100 |
| Other | unidentified | 100 |
| | coral | 67 |
| | tunicates | 89 |
| | shell | 11 |
| | fish | 11 |

Appendix 7: Other results, independent of feeding ecology.

In addition to the feeding ecology of the angelfish species *P.asfur* and *P.maculosus*, some other data were collected and these are briefly shown.

Wet body weight versus total body length

The wet body weight is related to the total length for all dissected fish of both species. The sample size of 2 for *P.asfur* was too small to give a reliable relation between these two parameters. *P.maculosus* has a sample size of 9 and the relation between the weight and length of the fish is iteratively determined and can be given by:

$$W = 0.22 * L^{2.3}$$

W = wet body weight (g)
L = total body length (cm)

The data for *P.maculosus* fit the exponential curve described by this relation ($r = 0.999$) (see figure 11).

An exponent of 3 leads to maintenance of a constant shape as the fish grows (Weatherley & Gill, 1987). The species *P.maculosus* has an exponent of 2.3, which points to a faster increase of the fish length than the body weight. This might be explained by the strongly laterally compressed shape of the body of *P.maculosus*, which keeps the volume increase and consequently the increase of the weight of the fish lower than expected.

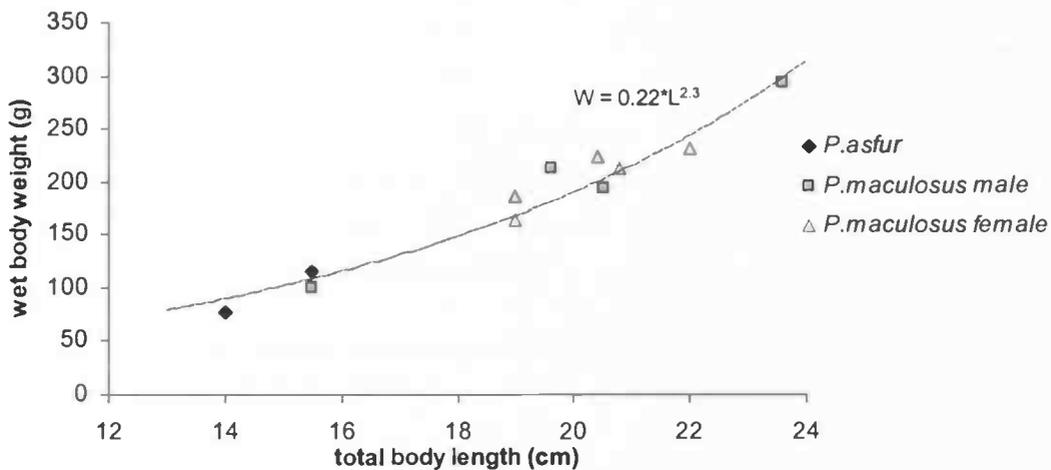


Figure 11: Wet body weight versus body length of the species *P.maculosus*.

GSI, LSI and FSI

The gonads, liver and fat tissue were weight immediately after the dissection of a fish, and a gonado-, liver- and fat-somatic index (respectively GSI, LSI and FSI) were calculated:

$$\text{GSI} = \text{wet gonad weight} \times 100\% / \text{total wet body weight}$$

$$\text{LSI} = \text{wet liver weight} \times 100\% / \text{total wet body weight}$$

$$\text{FSI} = \text{wet fat weight} \times 100\% / \text{total wet body weight}$$

Sexually active females can be expected to invest more energy in gamete production than males, since the production of eggs is energetically more expensive than that of sperm (Wootton, 1985). The relative gonad mass of the dissected females of *P.maculosus* was much higher than that of the males (Student's t-Test: $p = 0.016$; $\alpha = 0.05$) (see figure 12). Still, an average GSI of 0.19 % seems quite low compared to the 2 to 30 % values, commonly found for ripe females of many other species (Wootton, 1985). Additionally, spawning behaviour was not observed during the research period, so it might be that the fish were not in their fertile stage.

No differences are found between *P.maculosus* and *P.asfur* (Student's T-test: $p = 0.896$; $\alpha = 0.05$).

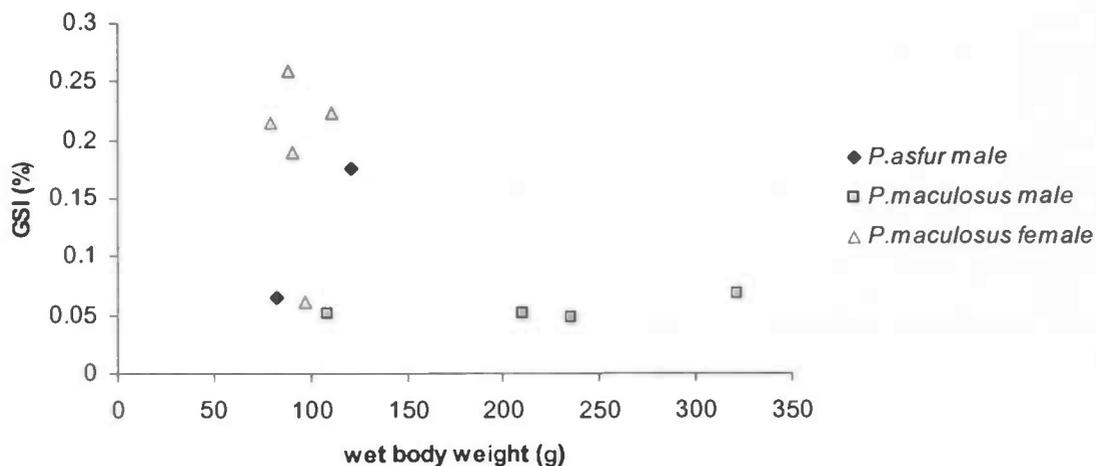


Figure 12: Gonado Somatic Index versus wet body weight for the individuals of *P.asfur* ($n=2$) and *P.maculosus* ($n=9$).

As shown in figure 13, liver somatic indexes of *P.asfur* and *P.maculosus* do not vary (Student's t-Test: $p = 0.061$; $\alpha = 0.05$). No differences are found between the males and females of *P.maculosus* as well (Student's t-Test: $p = 0.914$; $\alpha = 0.05$).

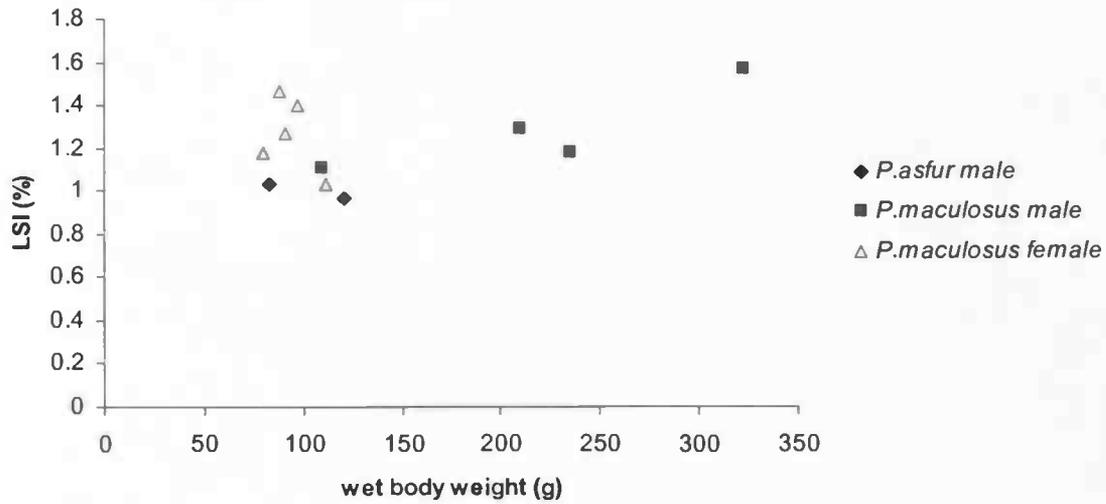


Figure 13: Liver Somatic Index versus wet body weight for the individuals of *P.asfur* ($n=2$) and *P.maculosus* ($n=9$).

In figure 14, *P.asfur* seems to contain relatively more fat than *P.maculosus*, but this is not statistically proven (Student's t-Test: $p = 0.224$; $\alpha = 0.05$). More research to enlarge the sample size is highly recommended, considering that there seems to be a big difference in the amount of fat tissue between the two species. No variation in relative fat content was found between the dissected males and females of *P.maculosus* (Student's t-Test: $p = 0.764$; $\alpha = 0.05$).

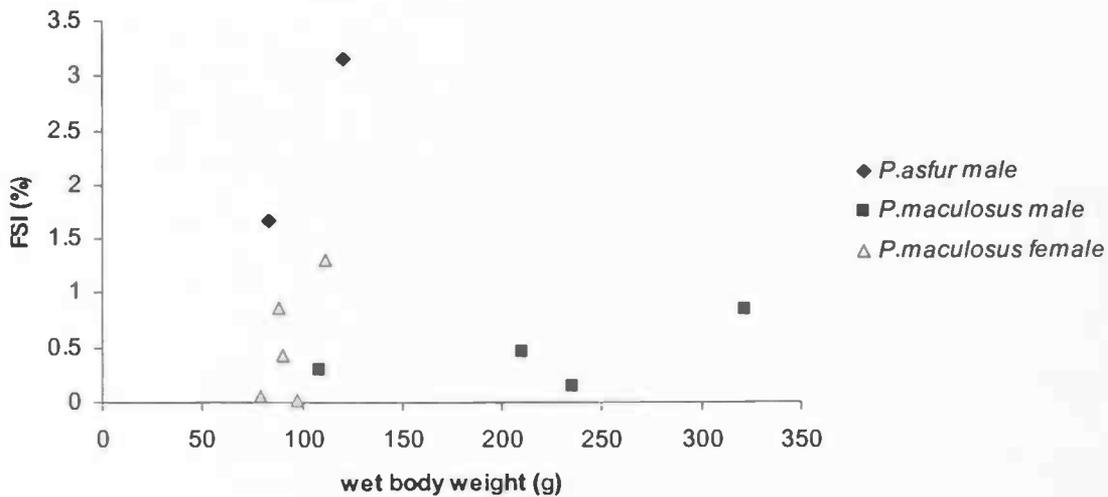


Figure 14: Fat Somatic Index versus wet body weight for the individuals of *P.asfur* ($n=2$) and *P.maculosus* ($n=9$).