

Aus dem Institut für Polarökologie
der Christian-Albrechts-Universität zu Kiel

**ECOLOGICAL STUDIES ON INTERTIDAL DOG WHELKS
(GASTROPODA: NASSARIIDAE) OFF NORTHERN MINAHASA,
SULAWESI, INDONESIA**

Dissertation
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Vorgelegt von

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Wisst ihr nicht, dass die, die in der Kampfbahn laufen, die laufen alle, aber einer empfängt den Siegespreis? Lauft so, dass ihr ihn erlangt

1 Kor. 9 : 24

Do you not know that in a race all the runners run, but only one gets the prize? Run in such a way as to get the prize

1 Cor. 9: 24

ERKLÄRUNG

Hiermit erkläre ich, dass die vorliegende Dissertation – abgesehen von der Beratung durch meine akademischen Lehrer – nach Inhalt und Form meine eigene Arbeit ist. Sie wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein erster Promotionsversuch.

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SUMMARY

Dog whelks (Gastropoda: Nassariidae) are prominent members of the intertidal fauna in both temperate and tropical regions. However, while there is quite a wealth of information on temperate nassariids, our information on tropical species has been rather scarce. Therefore, I have studied the intertidal dog whelk assemblages at three sites (Arakan, Mokupa, and Likupang), differing in their environmental setting (exposition, human impact), off the northern coast of the Minahasa Peninsula, North Sulawesi, Indonesia.

To assess the **spatial and temporal patterns** in the composition and distribution of the nassariid assemblages and key environmental parameters (water temperature, salinity) I took monthly samples, using a transect linear quadrat method, in three intertidal zones (upper, middle, and lower zone) between the high-water spring tide line and the low-water spring tide line over a one-year wet–dry season cycle (August 2000 to July 2001).

Seawater temperatures varied slightly from 30.3 to 34.8°C at Arakan, 29.4 to 33.8°C at Mokupa and 31.4 to 35.8°C at Likupang. **Salinities** in tide pools ranged from 27 to 35 at Arakan, 28 to 35 at Mokupa and 29 to 40 at Likupang. The **tides** were of the ‘mixed prevailing semi-diurnal’ type. The average tidal range was about 1.8 m.

A total of **eight nassariid species** were recorded during this study. Three of these (*Nassarius pullus*, *N. bimaculosus*, and *Hebra corticata*) occurred at all three sites, two (*N. globosus*, *N. luridus*) only at Arakan and Mokupa, and three (*N. camellus*, *N. venustus*, *N. livescens*) only at one site (Arakan and Likupang, respectively).

Nassariid monthly average **densities** ranged between about 12 ind.m² in the middle zone of Arakan (in August and December 2000) and the upper zone of Mokupa (in January 2001) and < 1 ind m² in the lower zones of Mokupa and Likupang. *H. corticata*, which was strictly coupled to the presence of sea grass, dominated the nassariid assemblages at sea-grass covered sampling sites (middle and lower zone at Arakan, all zones at Mokupa). At places without sea grass cover, either *N. globosus* (upper zone at Arakan) or *N. bimaculosus* (all zones at Likupang) were most important. Overall, *N. pullus* was most abundant, because it was the only species that occurred at each site and in each tidal zone. A 3-way ANOVA indicated that nassariid densities differed significantly among study sites as well as among intertidal zones: monthly average values were highest at Arakan (2.3 to 8.0 ind m²), followed by Mokupa (0.9 to 5.7 ind m²) and lowest at Likupang (0.3 to 3.5 ind m²), and they mostly decreased along the upper–middle–lower tidal gradient. However, the tidal main effect was confounded by a significant interaction between sites and zones, since at Arakan nassariid snails were most abundant in the middle (yearly average of 8.0 ind m²) instead of the upper zone (6.7 ind m²). Average abundances also differed significantly between seasons, with the wet season (November to January) featuring significantly higher densities than all other three seasons (dry: May to July; wet-dry transition: February to

April; dry-wet transition: August to October). This seasonal pattern was consistent in all three intertidal zones but not at all three sites.

The spatial and temporal **biomass** distribution exhibited a very similar pattern as the abundances. Total monthly average biomass ranged between > 400 mg ash-free dry weight (AFDW) m^{-2} in the upper zone of Arakan in February 2001 to < 1 mg AFDW m^{-2} in the lower zones of all three study sites. They also differed significantly among sites, zones, as well as seasons. Over the whole year, they were highest at Arakan (160.9, 156.6 and 19.4 mg AFDW m^{-2} in the upper, middle and lower zone, respectively), followed by Mokupa (95.2, 47.6 and 4.6 mg AFDW m^{-2} , respectively) and Likupang (99.9, 26.3 and 1.4 mg AFDW m^{-2} , respectively). At all three sites and in all three zones, there was a consistent seasonal pattern in the variation of biomass, with highest values occurring during the wet season.

Multivariate analyses indicated that in terms of nassariid **community composition** Likupang was clearly disparate from the other sites and also Arakan and Mokupa exhibited only little overlap. The intertidal zonation was clearly pronounced at Likupang and Arakan but not at Mokupa. The faunistic differences between sites and zones were primarily determined by pronounced spatial gradients in the distribution of *N. bimaculosus*, *H. corticata* and *N. luridus*. In contrast to the distinct spatial patterns at different scales (sites, zones), there was no clear seasonal trend in the temporal dynamics of the nassariid assemblages.

The **population dynamics** of *N. pullus* from Arakan and *N. bimaculosus* from Likupang were investigated by analysis of monthly size-frequency histograms. Shell lengths of *N. pullus* ranged from 6 to 21 mm-below. Throughout the study year, quite large individuals (= 16 mm-below) numerically dominated the samples of *N. pullus* and formed a very pronounced stationary mode at 18 mm-below. Other modes at smaller sizes, indicating younger cohorts, were markedly smaller, in some months they were even absent. In case of *N. bimaculosus*, ranging in size from 6 to 19 mm-below, a more dynamic development was visible. The mode representing the oldest and largest animals in the samples was not as pronounced and not as stationary as for *N. pullus*, and it was located at markedly smaller lengths (14 to 16 mm-below). Minor modes at smaller sizes were discernible in most months and could account for a considerable part of the sample. Thus, *N. bimaculosus* obviously reaches a smaller maximum length than *N. pullus*, and the population comprised more smaller and younger individuals.

The von Bertalanffy **growth** (VBG) parameters, which were estimated from the time series of the monthly size histograms to describe the individual growth of the two nassariid, were $L_{\infty} = 22.6$ mm, $K = 0.78$ year $^{-1}$ and $t_0 = -0.12$ year for *N. pullus*, and $L_{\infty} = 20.5$ mm, $K = 1.00$ year $^{-1}$ and $t_0 = -0.10$ year for *N. bimaculosus*. According to these growth models, the smallest individuals of *N. pullus* in the samples (shell length of 6 mm-below) recruited at an age of 4 months and those of *N. bimaculosus* (6 mm-below) at an age of 3 months, and the largest *N. pullus* specimens found (21 mm-below) had an age of 3.8 years while the largest *N. bimaculosus* individuals (19 mm-below) were almost 3 years old.

There is evidence that **recruitment** took place throughout the whole year in both *N. pullus* and *N. bimaculosus*. No pronounced seasonal recruitment pulses were discernible in the monthly size histograms. In both species, recruitment was higher in the wet and wet-dry intermediate seasons (at comparatively low temperatures and low salinities) and than in the dry season (at high temperatures and high salinities). However, correlation analysis suggested that the relationship between recruitment strength and both temperature and salinity is rather weak.

The yearly **mortality** rate was estimated from the descending right arms of the length-converted catch curves (LCCC approach). For *N. pullus* only specimens of a size of at least 17 mm-below and a (relative) age of 1.9 years were considered, while for *N. bimaculosus*, the lower boundary was 14 mm-below and 1.2 years, respectively. The mortality rate of *N. pullus* was $Z = 2.64 \pm 0.38 \text{ year}^{-1}$ ($\pm 95\%$ confidence interval CI), corresponding to a yearly mortality proportion of $93\% \text{ year}^{-1}$ (CI: 90 to $95\% \text{ year}^{-1}$). For *N. bimaculosus*, the Z value was $3.77 \pm 0.42 \text{ year}^{-1}$, which is equivalent of a yearly mortality proportion of $98\% \text{ year}^{-1}$ (CI: 96 to $98\% \text{ year}^{-1}$). Thus, the mortality of *N. bimaculosus* seems to be significantly higher than that of *N. pullus*.

The **longevity**, estimated by $3/K$ (where K is the growth coefficient of the VBG formula), was 3.85 years (46 months) for *N. pullus* and 3.00 years (36 months) for *N. bimaculosus*.

The **reproduction biology** of *N. pullus* from both Arakan and Likupang and *N. bimaculosus* from Likupang was studied from August to October 2002. Gonad development stages were determined by examination of histological gonad sections of individuals with shell lengths between 10 and 19 mm-below.

At both Arakan and Likupang, the smallest mature *N. pullus* had a shell length of 14 mm-below. Sizes at **maturity** (L_{50}) were 15 and 16 mm-below, respectively. *N. bimaculosus* from Likupang matured at a smaller size: the smallest mature specimens had shell lengths of 13 mm-below, and L_{50} was estimated to fall into the same size class.

The computation of **sex ratios** indicated that, in general, there were more females than males for both *N. pullus* and *N. bimaculosus*. However, this disparity was not significant in each month and for each species because of rather small sample sizes. In both Arakan and Likupang, a number of *N. pullus* specimens with size = 16 mm-below featured abnormal hermaphroditic gonads.

The examination of **gonad development stages** yielded two main results. First, in both species gametogenesis was not synchronized between the individuals but occurred throughout the entire three-month study period. Thus, quite high proportions of the mature population were always sexually active, indicating that spawning took place at any time between August and October – and possibly also throughout the whole year, as it is typical for tropical species in general. Second, most female gonads investigated contained gametes at different stages of development and there were only very few gonads in a 'post-spawning' condition, suggesting that both species are partial spawners, as it is also common among tropical benthic invertebrates.

ZUSAMMENFASSUNG

Reusenschnecken (Gastropoda: Nassariidae) gehören zu den auffälligen Vertretern der Gezeitenfauna in gemäßigten und tropischen Regionen. Im Unterschied zu den borealen Arten wissen wir aber recht wenig über die tropischen Reusenschnecken. Deshalb habe ich an der nördlichen Küste der Halbinsel Minahasa (Nord-Sulawesi, Indonesien) die nassariiden Gemeinschaften in drei ausgewählten Wattengebieten (Arakan, Mokupa und Likupang) untersucht, die sich in wichtigen Umweltbedingungen (Exposition, menschlicher Einfluss) unterscheiden.

Um die **räumlichen und zeitlichen Muster** in der Zusammensetzung und Verteilung der Reusenschnecken-Assoziationen sowie der wichtigsten Umweltparameter (Wassertemperatur, Salzgehalt) aufzunehmen, habe ich über einen Zeitraum von einem Jahr (August 2000 bis Juli 2001) in den drei Untersuchungsgebieten regelmäßig jeden Monat Proben genommen, die nach dem "line transect"-Verfahren in drei Gezeitenzonen (obere, mittlere und untere Zone) entlang eines intertidalen Gradienten zwischen der Springhochwasser- und der Springniedrigwasserlinie verteilt waren.

Die **Wassertemperaturen** schwankten während des Untersuchungszeitraums nur gering: von 30,3 bis 35,8°C in Arakan, von 29,4 bis 33,8°C in Mokupa und von 31,4 bis 35,8°C in Likupang. Die **Salzgehalte** in den Gezeitentümpeln variierten zwischen 27 und 35 in Arakan, 28 und 35 in Mokupa und 29 und 40 in Likupang. Die **Gezeitenrhythmus** war "gemischt, überwiegend halbtägig" (d.h. täglich traten zwei Hoch- und zwei Niedrigwasser auf, jedoch in Abhängigkeit von der Mondphase mit starken Ungleichheiten in Höhe und Zeit). Der durchschnittliche Tidenhub betrug in allen drei Untersuchungsgebieten 1,8 m.

Insgesamt **acht Arten** Reusenschnecken wurden gefunden. Davon kamen drei Arten (*Nassarius pullus*, *N. bimaculosus* und *Hebra corticata*) in allen drei Gebieten vor, zwei Arten (*N. globosus* und *N. luridus*) waren nur in Arakan und Mokupa zu finden, und drei Arten (*N. camellus*, *N. venustus* und *N. livescens*) waren nur in jeweils einem Gebiet (Arakan bzw. Likupang) vertreten.

Die mittleren monatlichen **Besiedlungsdichten** der Reusenschnecken lagen zwischen maximal 12 ind m² in der mittleren Zone in Arakan (im August und Dezember 2000) sowie der oberen Zone in Mokupa (im Januar 2001) und minimal < 1 ind m² in den unteren Zonen in Mokupa und Likupang. Die Art *H. corticata*, die in ihrem Vorkommen streng an das Vorkommen von Seegras gekoppelt war, dominierte die Reusenschneckenfauna an Seegras-bewachsenen Standorten (mittlere und untere Zone in Arakan, alle Zonen in Mokupa). An Stellen ohne Seegrasbewuchs waren entweder *N. globosus* (obere Zone in Arakan) oder *N. bimaculosus* (alle Zonen in Likupang) dominierend. *N. pullus* kam als einzige Art in allen Untersuchungsgebieten und allen Gezeitenzonen vor und was deshalb insgesamt am abundantesten. Eine 3-Weg-ANOVA ergab, dass sich die mittleren monatlichen Besiedlungsdichten signifikant zwischen

den Untersuchungsgebieten und Gezeitenzonen unterschieden: die Werte waren in Arakan am höchsten (2,3 bis 8,0 ind m⁻²), gefolgt von Mokupa (0,9 bis 5,7 ind m⁻²) und Likupang (0,5 und 3,5 ind m⁻²); außerdem nahmen die Besiedlungsdichten in der Regel von der oberen zur unteren Zone hin deutlich ab (nur in Arakan waren die jährlichen mittleren Dichten in der mittleren Zone (8,0 m⁻²) höher als in der oberen Zone (6,7 m⁻²)). Die mittleren Abundanzen unterschieden sich auch zwischen den Jahreszeiten: sie waren während der Regenzeit (November bis Januar) signifikant höher als in den anderen drei Jahreszeiten (Trockenzeit: Mai bis Juli; Regen-Trocken-Übergangszeit: Februar bis April; und Trocken-Regen-Übergangszeit: August bis Oktober). Dieses saisonale Muster war in allen drei Gezeitenzonen, aber nicht in allen drei Untersuchungsgebieten zu finden.

Die **Biomassen** zeigten ein sehr ähnliches räumliches und zeitliches Muster wie die Abundanzen. Die monatlichen Mittelwerte schwankten zwischen > 400 mg aschefreies Trockengewicht (AFTG) m⁻² in der oberen Zone in Arakan im Februar 2001 und < 1 mg AFTG m⁻² in den unteren Zonen aller drei Untersuchungsgebiete. Es gab signifikante Unterschiede zwischen den Untersuchungsgebieten, Gezeitenzonen und Jahreszeiten (3-Weg-ANOVA). Über das ganze Jahr betrachtet, waren die nassariiden Biomassen in Arakan am höchsten (160,9 mg, 156,6 mg und 19,4 mg AFTG m⁻² in der oberen bzw. mittleren bzw. unteren Zone), gefolgt von Mokupa (95,2 mg bzw. 47,6 mg bzw. 4,6 mg AFTG m⁻²) und Likupang (99,9 mg bzw. 26,3 mg bzw. 1,4 mg AFTG m⁻²). In allen Untersuchungsgebieten und allen Gezeitenzonen gab es ein konsistentes saisonales Muster in der zeitlichen Variabilität der Biomassen, mit signifikant höheren Werten während der Regenzeit.

Multivariate Datenanalysen zeigten, dass sich Likupang hinsichtlich der **Artenzusammensetzung** der Reusenschneckenfauna deutlich von den anderen Untersuchungsgebieten unterschied und dass es auch zwischen Arakan und Mokupa nur relativ geringe Übereinstimmung gab. Die intertidale Zonierung in der Verteilung der Gemeinschaften war in Likupang und Arakan deutlich ausgeprägt, in Mokupa jedoch nicht. Die faunistischen Unterschiede wurden vor allem durch die Gradienten in der Verteilung der Arten *N. bimaculosus*, *H. corticata* und *N. luridus* bestimmt. Im Unterschied zu den deutlichen räumlichen Mustern auf verschiedenen Skalen (Untersuchungsgebiete, Gezeitenzonen) konnte kein klarer saisonaler Trend in der zeitlichen Dynamik der nassariiden Gemeinschaften festgestellt werden.

Die **Populationsdynamik** von *N. pullus* in Arakan und *N. bimaculosus* in Likupang wurde durch die Analyse von Zeitserien monatlicher Größen-Häufigkeits-Verteilungen untersucht. Die Schalenlängen (gemessen auf den unteren mm) von *N. pullus* lagen in einem Bereich zwischen 6 und 21 mm. Während des gesamten Untersuchungsjahrs dominierten relativ große Individuen (= 16 mm) zahlenmäßig in den Proben und bildeten eine sehr ausgeprägte, konstante Verteilungsmode bei 18 mm. Weitere Moden bei geringeren Größen, die jüngere Kohorten anzeigten, waren deutlich kleiner und fehlten in manchen Monaten gänzlich. Bei *N. bimaculosus*, deren Größen zwischen 6 und 19 mm lagen, war eine größere Dynamik in der Veränderung der

Größen-Häufigkeits-Verteilungen zu beobachten. Die Mode, die die ältesten und größten Individuen in den Proben repräsentierte, war nicht so ausgeprägt wie bei *N. pullus*, lag bei deutlich geringeren Größen und variierte mehr im Jahresgang (zwischen 14 und 16 mm). Niedrigere Moden bei kleineren Schalenlängen waren in den meisten Monaten klar erkennbar und repräsentierten einen erheblichen Prozentsatz der gesamten Proben. *N. bimaculosus* erreichte demnach eine geringere Endgröße als *N. pullus*, und die Population bestand zu einem höheren Anteil aus kleinen und jungen Individuen.

Das von-Bertalanffy-Wachstum-Modell (VBW) wurde benutzt, um das individuelle Wachstum der beiden Reusenschneckenarten zu beschreiben. Die Parameter der VBW-Funktion wurden aus den Daten der monatlichen Größen-Häufigkeits-Verteilungen abgeleitet: sie lauteten $L_{\infty} = 22,6$ mm, $K = 0,78$ Jahr⁻¹ und $t_0 = -0,12$ Jahr für *N. pullus* und $L_{\infty} = 20,5$ mm, $K = 1,00$ Jahr⁻¹ und $t_0 = -0,10$ Jahr für *N. bimaculosus*. Die kleinsten gefundenen Individuen von *N. pullus* (6 mm) wären demnach 4 Monate und die von *N. bimaculosus* (6 mm) 3 Monate alt gewesen, während die größten Exemplare von *N. pullus* (21 mm) ein Alter von 3,8 Jahren und die von *N. bimaculosus* (19 mm) von fast 3 Jahren hatten.

Nach meinen Befunden fand während des gesamten Untersuchungsjahres in beiden Populationen eine **Rekrutierung** junger Individuen statt. In den monatlichen Größen-Histogrammen gab es keine Indizien für ausgesprägte saisonale Rekrutierungspulse. Tendenziell war die Rekrutierung bei beiden Arten in der Regen- und Regen-Trocken-Übergangszeit (bei relativ niedrigen Temperaturen und Salzgehalten) größer als in der Trockenzeit (mit hohen Temperaturen und Salzgehalten), aber die Korrelationen zwischen relativer Rekrutierungsstärke und beiden Umweltfaktoren (Temperatur, Salzgehalt) waren nur relativ schwach und meist statistisch nicht signifikant.

Die jährliche **Sterblichkeitsrate** Z wurde aus der Steigung der abfallenden rechten Seiten der "length-converted catch curves" (LCCC) bestimmt. Für *N. pullus* wurden dabei nur Individuen einer Mindestgröße von 17 mm und einem (relativen) Mindestalter von 1,9 Jahren berücksichtigt. Für *N. bimaculosus* lauteten die entsprechenden Grenzen 14 mm bzw. 1,2 Jahre. Als Sterblichkeitsrate von *N. pullus* wurde $Z = 2,64$ Jahr⁻¹ ($\pm 0,38$ Jahr⁻¹ 95%-Vertrauensbereich VB) geschätzt, was einer prozentualen Sterblichkeit von 93% Jahr⁻¹ (VB: 90 bis 95% Jahr⁻¹) entspricht. Die entsprechenden Werte von *N. bimaculosus* waren $Z = 3,77$ Jahr⁻¹ ($\pm 0,42$ Jahr⁻¹ VB) und 98% Jahr⁻¹ (VB: 96 bis 98% Jahr⁻¹), d.h. die Sterblichkeit von *N. bimaculosus* war signifikant größer als die von *N. pullus*.

Die **Lebenserwartung**, geschätzt durch den Wert von $3/K$ (wobei K der Wachstumsparameter der VBW-Funktion ist), betrug für *N. pullus* 3,85 Jahre (46 Monate) und für *N. bimaculosus* 3,00 Jahre (36 Monate).

Die **Reproduktionsbiologie** von *N. pullus* aus Arakan und Likupang und von *N. bimaculosus* aus Likupang wurde während eines dreimonatigen Zeitraums von August bis Oktober 2002 untersucht. In histologischen Schnitten wurde dazu das Geschlecht und die

verschiedenen Entwicklungsstadien der Gonaden von Tieren mit Schalenlängen zwischen 10 und 19 mm bestimmt.

Sowohl in Arakan als auch in Likupang wurde *N. pullus* ab einer Minimalgröße von 14 mm **geschlechtsreif**. Ab einer Größe von 15 bzw. 16 mm (L_{50}) waren 50% aller untersuchten Exemplare geschlechtsreif. *N. bimaculosus* erreichte die Geschlechtsreife früher ($L_{50} = 13$ mm).

Bei der Bestimmung der **Geschlechterverhältnisse** zeigte sich, dass es sowohl für *N. pullus* als auch für *N. bimaculosus* mehr Weibchen als Männchen gab. Dieser Trend war jedoch wegen der geringen Stichprobengrößen nicht in jedem Monat statistisch signifikant. Etliche Exemplare von *N. pullus* aus beiden Untersuchungsgebieten hatten ab Größen von = 16 mm abnormale hermaphroditische Gonaden.

Die Untersuchung der **Gonadenstadien** hatte zwei Hauptergebnisse: Erstens war bei beiden Arten die Gametogenese während des gesamten dreimonatigen Untersuchungszeitraums nicht zwischen den Individuen einer Population synchronisiert. Daher war immer ein relativ großer Teil der Population sexuell aktiv, was darauf hindeutet, dass zu jeder Zeit von August bis Oktober Laichen stattfand. Dies kann als Indiz gewertet werden, dass prinzipiell während des gesamten Jahres gelaicht werden kann, wie es für viele tropische Arten typisch ist. Zweitens enthielten die Gonaden der meisten untersuchten Weibchen beider Arten Gameten in unterschiedlichen Entwicklungsstadien und es wurden nur relative wenige Gonaden in einem vollständig abgelaichten Zustand gefunden. Dieser Befund deutet darauf hin, dass sowohl *N. pullus* als auch *N. bimaculosus* Teil-Laicher sind, also sukzessive in mehreren Schüben laichen. Diese Reproduktionsstrategie ist ebenfalls bei vielen benthischen tropischen Evertrebraten verbreitet.

Chapter 1

GENERAL INTRODUCTION

1.1 Research on tropical benthos

Several studies have addressed the macrobenthos in tropical areas, either specifically (e.g. Malaysia: Vohra 1971, Broom 1981; Australia: Dittmann 1995, 2000; Kenya: Schrijvers et al. 1995) or in the framework of broad inter-latitudinal comparisons (Warwick & Ruswahyuni, 1987; Alongi 1989, 1990; Reise, 1991; Dittmann & Vargas, 2001). In addition, several experimental studies have been conducted on molluscs, especially on bivalve species that are economically important (e.g. Vietnam: Le Duc Minh, 1999; Vo Si Tuan, 1999; Thórarinsdótti, 1999; Indonesia: Omar & Yulianda, 2000; Thailand: Banchungmanee & Upanoi, 2000; Upanoi & Banchungmanee, 2000; South China: Yasin & Tan Shau-Hwai, 2000) but also on gastropods (e.g. Indonesia: Kohn, 1998; Boneka et al., 1999; Malaysia: Tan, 1999; Vietnam: Ngo Anh Tuan, 2000).

Most scientists focussed their attention on hard-bottom substrates, especially coral reefs, or mangroves. In contrast, intertidal flats were clearly less intensively investigated, even though these soft-sediment environments also provide habitats for a quite diverse and abundant benthic fauna. Reid (1967) stated that along the coasts where sea and land meet natural forces have combined to produce what are probably the richest and most varied communities of plants and animals to be found anywhere. Within the Indo-Pacific region, which is in general known as a hotspot of biodiversity, Indonesian waters are richest in molluscs species (Soemodihardjo & Kastoro, 1982). On tropical intertidal flats, prosobranch gastropods are usually the most prominent taxon, both in terms of abundance and with respect to individual size, and within this group most species are active predators (Taylor, 1986). However, little is known about their distribution, abundance, growth and reproduction, especially with regard to the scavenging dog whelk species of the neogastropod family Nassariidae.

1.2 Distribution of the gastropod family Nassariidae

Dog whelks (Nassariidae) belong to the most common soft-sediment prosobranchs. They are widely distributed along the Pacific coasts of the Americas, as well as along the West Atlantic-Caribbean, European, East Atlantic and Indo-Pacific shores (Cernohorsky, 1984). Nassariids not only occur over a wide geographical range but also often play a dominant role in benthic communities. They live primarily on estuarine to shallow marine soft substrates, usually in tropical and temperate regions, and attain their greatest diversity in the tropical Indo-Pacific (Pepping et al., 1997). These snails can move quite rapidly, sliding along the sand or mud

waving their siphon from side to side as they search for food. They can also bury themselves remarkably quickly into the sediment by flexing and arching the body (Wilson, 1994).

A total of 211 extant species of the genus *Nassarius* have been reported from Indo-Pacific waters (Cernohorsky, 1984). In Indonesian waters, several rare *Nassarius* species were found in western Java and western Sumatra (Kool, 1992), and in Irian Jaya even more new species were discovered (Kool, 1996). During the "Rumphius Biohistorical Expedition" to Ambon in 1990 (Kool & Strack, 2000) a total of 47 species were found.

1.3 Motivation

Most attention of marine biologists studying dog whelk ecology has been directed to long-term sampling surveys of temperate *Nassarius* species (e.g. Fioroni et al, 1990; Barroso & Moreira, 1998; Demaintenon, 2000a, 2000b; Bareiro et al, 2001). These investigations generally indicated that *Nassarius* species is a potential bioindicator species for environmental monitoring, since they have a key role in the intertidal communities and especially sensitive to the environmental changes.

Dog whelks are known for developing in response to certain environmental stress stimuli a peculiar abnormality of their genital organs, which involves a superimposition of male characteristics on to a functionally normal female reproductive anatomy. This phenomenon, called 'imposex', has been discovered by Smith (1971) when studying the dioecious American mud dog whelk *Nassarius obsolatus* Say. Recently, a total of 51 prosobranch species have been listed to feature 'imposex', including 5 species of *Nassarius* (Fioroni et al, 1990).

Nassarius species were anecdotically known to be quite diverse and abundant at the intertidal flats off the northern Minahasa Peninsula, Indonesia. However, there was no quantitative information on their spatial and temporal distribution and population dynamics, and a variety of questions about ecological and biological aspects were also unknown so far.

This study did not take place in the pristine wilderness but in an inhabited area. It is quite true that the developing countries currently assign a higher priority to food production and economic development than to conservation issues. The mining of corals or collection of seaweed and ornamental shells is of considerable economic importance for many coastal settlements in the tropics. Under such circumstances, it is difficult to find a reasonable compromise between the protection of bio-diversity and the conservation and sustainable management of the natural resources on the one hand and the need for survival of the people on the other. The results of the present study provide ecological information on predominant *Nassarius* species in the intertidal flats off Northern Minahasa Peninsula, which will be useful for a possible sustainable management in case these dog whelks will be exploited as a natural

resource in the future. Thus, my investigation offers a model for forthcoming studies in other areas and/or other intertidal species.

1.4 Objectives

There are two main purposes of the present study:

- (1) to investigate the ecology of nassariids assemblages in the intertidal flats off the northern Minahasa Peninsula
- (2) to extend the knowledge of the population dynamics and biology of predominant species

To address these issues, field data were gathered once each month throughout one year along the intertidal gradient at three selected sites differing in their environmental setting.

The results gathered in my study are presented in separate chapters. Chapter 2 describes the study area, chapter 3 deals with the spatial and temporal distribution patterns, chapter 4 provides information on growth, recruitment pattern, mortality and longevity, and the stages of gonad development are presented in Chapter 5.

Chapter 2

STUDY AREA

The study was conducted at the northern coast of the Minahasa Peninsula, North Sulawesi, Indonesia. Two intertidal sites were selected: Arakan and Mokupa at the south-western and Likupang at the northeastern coast of Manado city (Figure 2.1).

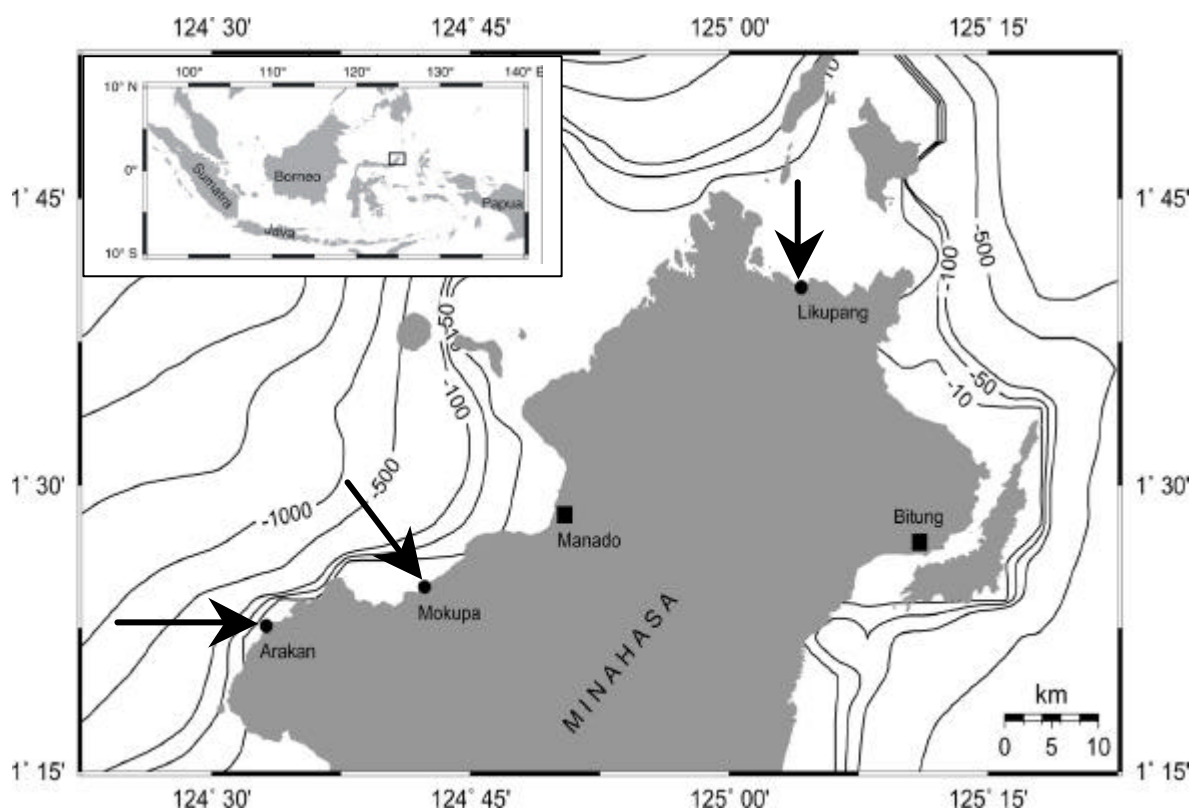


Figure 2.1. Map of the Northern Minahasa Peninsula, North Sulawesi - Indonesia. The study sites are marked by the arrows. Water depths are in meters.

2.1 Description of study sites

Arakan is a small fishing village located at $1^{\circ}22'35''$ N and $124^{\circ}33'10''$ E (Figure 2.2). The coastal area is characterized by an intertidal region, featuring extensive riverine mud-sand plains and offering good growth conditions for mangrove assemblages. The shore slopes gently from the high tide level which is marked by sparsely growing grass and coconut palms.

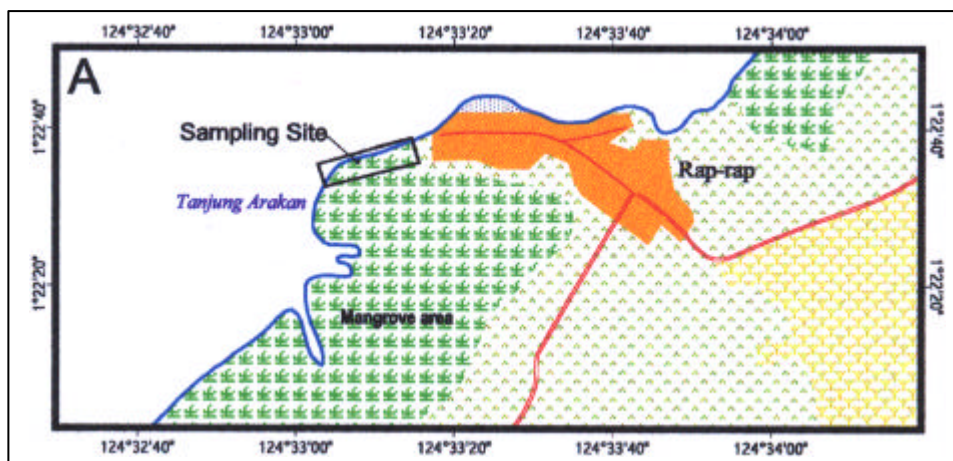


Figure 2.2. Sampling site of Arakan.

Seawards, about 70-100 m a narrow belt of mangroves and then broad wadden zone. A vertical section of the mud showed a top dark brown layer (0.5–5 cm thick) covering black sand. This area is well-drained at low tide, except for some small pools and furrows. At the spring low water line, there is zone characterised by very soft bottom and the occurrence of seagrass beds (*Halophila ovalis*, *Enhallus accoroides*, *Thalassia hemprichii* and *Cymodocea rotundata*), which provide habitats for a great variety of sea life. Beyond this zone, there is closed area of seaweed cultures and its bounded by a bench of rough reef limestone formed by mostly dead corals.

The tidal flats off Mokupa (1°24'37" N and 124°42'20" E) form a 70 – 100 m wide fringe between a supra-littoral mangrove belt and the low water line (Figure 2.3). About 300 m to the north, there is an extensive estuary in the mouth of a small stream.

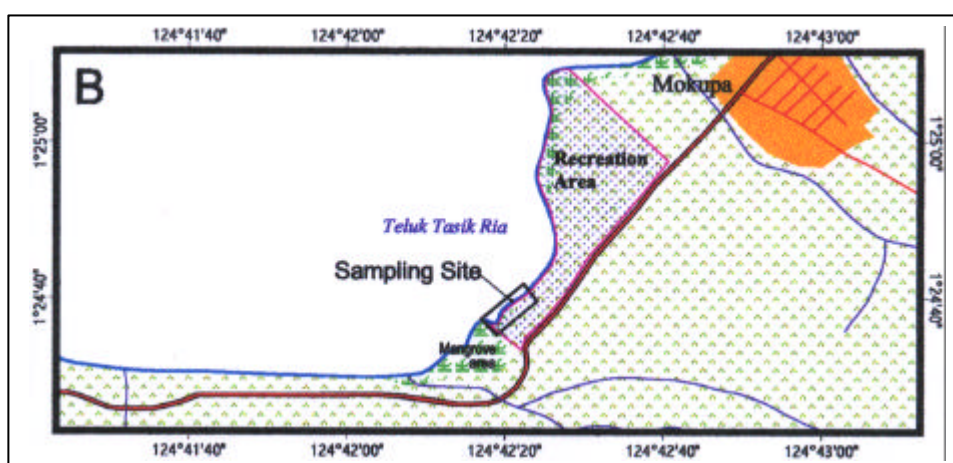


Figure 2.3. Sampling site of Mokupa.

The tidal sediments mostly consist of sandy mud with occasional shell gravel inclusions. The tidal flat slopes gently from the high water line which is marked by coconut palms and mangroves (*Sonneratia* sp). Various seagrass species, such as *Enhallus accoroides*, *Thalassia hemprichii* and *Syringodium isoetifolium* grow on the flat, albeit only in patches. A bench of rough reef limestone, made up by coral pabble and colonised by sparsely growing seaweed (*Gracilaria* sp and *Amphiroa fragilissima*), defines the seaward boundary of the intertidal flat.

Likupang site located near the Field Station of Universitas Sam Ratulangi is closed to Likupang village (1°40'22" N and 25°4'18" E). The area was selected because it is easy to reach and differs from the other two sites in sediment (sand instead of silt) and degree of anthropogenic impact. It is characterised by a gently sloping bottom from the high water line, which is marked by densely growing grass and coconut palms. Only few mangroves and seagrass were found at the northern and southern edges of the study area. An 80-300 m broad tongue-shaped sand flat extends from the mouth of the "Kuala Mati" (termed for "river") 1 km westwards along the coastline (Figure 2.4).

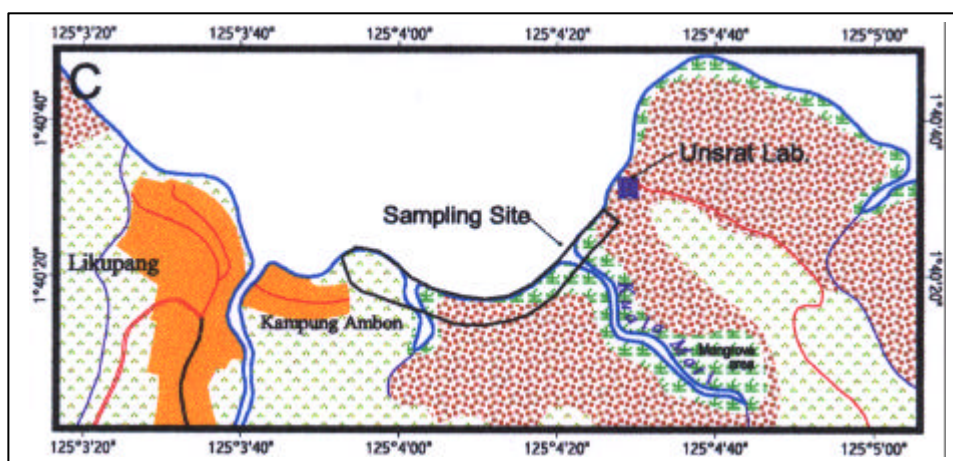


Figure 2.4. Sampling site of Likupang

2.2 Climate

The climate in the study area is strongly affected by the monsoon wind system. In general, there are two major seasons: a wet and a dry season, which are separated by transition periods. During the transition to wet season (November to April), relatively cool northwesterly winds blow over the South China Sea and bring much moisture to North Sulawesi. During the dry season from June until September, southwesterly steady, light to moderate winds originating from the Australian land mass lead to higher temperature and reduced precipitation. The short

transition periods (April - May and October - November) feature weak and unsteady winds (Tomascik et al., 1997).

The total rainfall in the northern section of the Park reaches 3,000-3,500 mm with 2,200 mm during the wet season and 1,100 mm during the dry season. Average monthly rainfalls (1977 – 2000) North Sulawesi Province, varied from 130 mm (August) to 389 mm (December). Between October and June, monthly precipitation exceeded 200 mm. The dry to transition seasons months July, August and September featured rainfall less than 200 mm. The average monthly air temperature varied only slightly from 25.2°C in February to 26.5°C in August (Figure 2.5). Tomascik et al (1977) concluded that the average sea surface temperatures in coastal waters range between 27° and 29°C throughout the year. However, temperatures can easily exceed 30°C in intertidal pools at low tide (own observations).

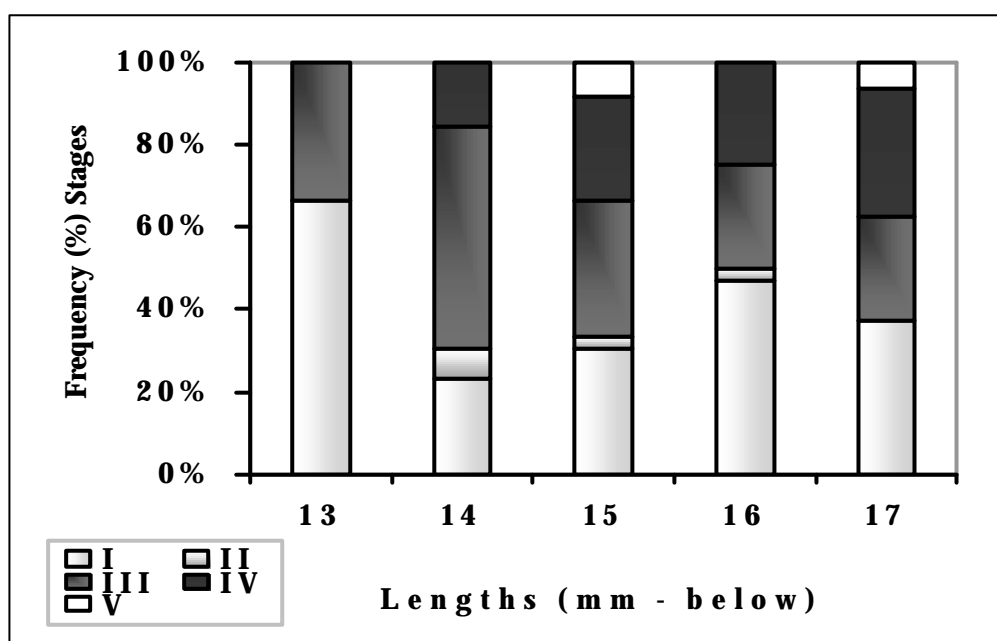


Figure 2.5. Rainfall and average monthly air temperature near the northern Bunaken National Park (1°30 N and 124°5 4' E, elevation 67m). Source Manado Meteorology and Geophysic, 2001.

2.3 Hydrography

The tides around Sulawesi Island are defined as “mixed prevailing semi-diurnal” (Tomascik et al., 1997), meaning that two high and two low tides occur each day. The average tidal range is about 1.8 m.

From January to April currents flow north-eastward at maximum speeds of up to 5 km/h. In July the direction of the currents changes south-westward although there is small change in speed. In October, currents generally run westward (Anonymous, 1991).

From the limited field observations undertaken during this study, it can be concluded that there are usually two main coastal currents off Arakan and Mokupa: a southwest current during the dry season (May, June and July) and a north current during the wet season (November, December and January). Off Likupang, the current patterns are more complex due to the presence of off shore islands.

When seawater enters the intertidal zone during flood, its speed and direction are largely determined by the local intertidal landscape. At Arakan and Mokupa, the seawater enters and exits the intertidal area through indentations in the fringe reefs and flows through shallow tidal channels that regularly dissect the tidal flat. At Likupang, the tide movements are generally faster due to the absence of a barrier reef.

Chapter 3

SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS

3.1 Introduction

Several authors have studied various aspects of temperate intertidal *Nassarius* species. For example, there have been a number of investigations on *N. obsoletus*, dealing with the significance of salinity as ecological factor (Bergmann & Graham, 1975), the relationship to periwinkles (Dippolito et al., 1975), the physiological ecology of larvae (Vernberg & Vernberg, 1975), and adaptations in egg development (Pechenik, 1978). The effects of feeding and substrate selection for egg-capsule deposition of *N. reticulatus* were reported by Crisp (1978) and Barnett et al. (1980). For the Australian species *N. pauperatus* behaviour (McKillup, 1983) and long-term ecology (McKillup et al., 1993 and 1995) has been studied. In comparison, only a few species from subtropical areas have been studied. Morton (1990) investigated the physiology and feeding behaviour of *N. festivus*; Morton and Chan (1999) reported about predation on the subtidal scavenger *N. siquijorensis*; Morton and Yuen (2000) studied feeding behaviour and competition for carrion between *N. festivus* and the hermit crab *Diogenes edwardsii*, and Tomoki & Hiroyuki (1996) redescribed the species *N. cinnamomea*, which is abundant in submarine caves of Okinawa.

Tropical nassariids were even more rarely studied. If there is information at all, then it has been mostly gathered in the frame of benthic community surveys (Vohra, 1971; Broom, 1982; Dittmann & Vargas, 2001). Apart from this, the structure of local populations and their spatial and temporal variability in tropical intertidal soft-bottom habitats are virtually unknown. Therefore, the prime interest in this study was to collect general information on nassariid distribution and biology in a tropical region. A basic description of the composition, distribution, abundance and biomass of dog whelk assemblages at three intertidal flats off Northern Minahasa Peninsula, Indonesia, is presented in this chapter.

The results of this study also compared between latitudes based on the some general ideas derived from ecological studies in temperate tidal flats: 1) species diversities are higher in tropical than in temperate tidal flats while abundances are lower; 2) within the intertidal zone, the distribution of benthic organisms usually follows a zonation in response to varying environmental conditions in sediment composition, wave exposure and duration of submergence and exposure (Sanders et al., 1962).

3.2. Material and methods

3.2.1 Field sampling

The intertidal flats off Arakan, Mokupa and Likupang were surveyed monthly from August 2000 to July 2001 for the presence of nassariid snails. To assess the distribution along the tidal gradient between high and low water level, samples were taken along three (Arakan and Likupang) or two transects (Mokupa), which were perpendicular to the coastline. The distance between the transects were 200 m at Arakan, 50 m at Mokupa and 300 m at Likupang. The transects were divided into three different sections (upper, middle and lower) between the mean high water spring tide line (MHWS) and the mean low water spring tide line (MLWS) (Table 3.1).

Table 3.1. Range of the intertidal zones (distances in metres from the mean high water spring tide line (MHWS))

Site	Zones		
	Upper (m)	Middle (m)	Lower (m)
Arakan	0 - 50	50 - 100	100 - 170
Mokupa	0 - 40	40 - 80	80 - 120
Likupang	0 - 60	60 - 120	120 - 200

Sampling was carried out during low spring tides. Along the line transects, 1 x 1 m quadrates were placed at 10 m intervals. The upper 10 cm layer of the sediment within the quadrates was sieved through a 1mm mesh. Because of the difficulty of shovelling the sediments accurately in case of water still covering the flat bottom in tide pools, the following procedure was adopted: first four shovels of the surface layer of sand, each starting at one corner of the quadrate, thereafter four shovels of the remaining sediment, and finally one shovel from the centre of the quadrate were sieved. All snails were collected from the sieve residue, as well as any specimen observed on the surface of the quadrate, and fixed in 4% borax-buffered formalin. Empty shells and organisms considered dead at the time of sampling were excluded from subsequent analyses.

In total, 437 samples were taken off Arakan, 183 off Mokupa and 380 off Likupang (Table 3.2). All samples were brought to the laboratory, where all nassariid specimens were identified to species level and counted.

Table 3.2. List of samples collected during the study period between August 15, 2000, and July 7, 2001, at three sampling sites (Arakan, Mokupa and Likupang).

Arakan

Sampling Date	No. of quadrates	No. of Species	No. of Individuals	Moon phase	Season
15 August 2000 (11:00 AM)	34	4	375	Full moon	Dry
12 September 2000 (11:00 AM)	35	5	271	Full moon	Transition
12 October 2000 (11:00 AM)	36	5	181	Full moon	Transition
12 November 2000 (11:00 AM)	35	5	223	Full moon	Transition
12 December 2000 (11:00 AM)	33	5	352	Full moon	Wet
11 January 2001 (11:00 AM)	30	5	305	Full moon	Wet
11 February 2001 (12:00 AM)	37	5	302	Last quarter	Wet
10 March 2001 (11:00 AM)	34	5	284	Full moon	Transition
08 April 2001 (10:00 AM)	38	6	310	Full moon	Transition
05 May 2001 (10:00 AM)	43	6	232	Full moon	Transition
06 June 2001 (11:00 AM)	42	6	199	Full moon	Dry
05 July 2001 (11:00 AM)	40	6	198	Full moon	Dry

Mokupa

Sampling Date	No. of quadrates	No. of Species	No. of Individuals	Moon phase	Season
17 August 2000 (11:00 AM)	22	4	63	Full moon	Dry
14 September 2000 (11:00 AM)	17	4	101	Full moon	Transition
14 October 2000 (11:00 AM)	9	4	38	Full moon	Transition
14 November 2000 (12:00 AM)	16	4	108	Last quarter	Transition
14 December 2000 (13:00 AM)	17	4	145	Full moon	Wet
13 January 2001 (13:00 AM)	15	4	152	Last quarter	Wet
13 February 2001 (14:00 AM)	16	5	67	Last quarter	Wet
12 March 2001 (12:00 AM)	15	5	38	Full moon	Transition
10 April 2001 (12:00 AM)	12	5	39	Full moon	Transition
07 May 2001 (11:00 AM)	18	4	70	Full moon	Transition
08 June 2001 (13:00 AM)	12	4	69	Full moon	Dry
07 July 2001 (13:00 AM)	14	3	52	Full moon	Dry

Likupang

Sampling Date	No. of quadrates	No. of Species	No. of Individuals	Moon phase	Season
16 August 2000 (11:00 AM)	25	2	79	Full moon	Dry
13 September 2000 (11:00 AM)	34	2	111	Full moon	Transition
13 October 2000 (11:00 AM)	29	1	68	Full moon	Transition
13 November 2000 (11:00 AM)	29	3	128	Full moon	Transition
13 December 2000 (11:00 AM)	30	3	119	Full moon	Wet
12 January 2001 (12:00 AM)	31	3	118	Last quarter	Wet
12 February 2001 (13:00 AM)	30	2	102	Last quarter	Wet
11 March 2001 (11:00 AM)	38	3	113	Full moon	Transition
09 April 2001 (12:00 AM)	30	2	52	Full moon	Transition
06 May 2001 (10:00 AM)	21	2	77	Full moon	Transition
07 June 2001 (11:00 AM)	35	3	74	Full moon	Dry
06 July 2001 (11:00 AM)	48	3	138	Full moon	Dry

3.2.2 Measurement of environmental variables

Temperature and salinity were monitored monthly in tide pools in order to provide environmental background information. Temperature was measured to the nearest 0.1 °C. A refractometer was used to determine salinity to the nearest 0.1. In addition, both variables were measured at the same time when snails were collected.

3.2.3 Determination of body size and biomass

The shell length (defined as the maximum distance between the apex of the shell to the anterior end of the lip) and width of every specimen were measured to the nearest 0.01 mm using vernier callipers. In addition, its wet weight, both with and without shell, was determined using a Sartorius Micro-Balance with a precision of 0.1 mg.

Ash-free dry weights (AFDW) were assessed according to the method proposed by Palmerini & Bianchi (1994). Shell-less specimens were pooled for species and transect, placed in aluminium dishes and dried for 24 hours at room temperature to obtain their dry weights (DW). AFDW was determined after incinerating them for 2 hours at 500°C in a muffle furnace and subsequently weighing their ash. Both DW and ash weights were determined with a precision of 0.1 mg using a Sartorius Micro-Balance. Because nassariids snails are too small to be weighed individually, specimens from each species and each transect were pooled.

3.2.4 Statistical analyses

3.2.4.1 Analyses of variance

A three-way analysis of variance (ANOVA) was performed to determine whether significant differences in total nassariid density and biomass occurred between:

- 1) Sites: Arakan, Mokupa, and Likupang
- 2) Zones: upper, middle, and lower zone (nested within Sites)
- 3) Seasons: dry (May, June, July), dry-wet intermediate (August, September, October), wet (November, December, January), and wet-dry intermediate (February, March, April)

Prior to analyses, abundance and biomass values were averaged across transect sections (upper, middle and lower) and then $\log(x+1)$ transformed to achieve homogeneity of variances.

3.2.4.2 Multivariate analyses

Multivariate analyses of the multi species data sets were performed by means of the software package PRIMER 5.2 (Plymouth Routines in Multivariate Ecological Research; Clarke & Warwick, 1994). Analysis of similarities (ANOSIM) was used to test whether species composition of nassariid assemblages differed significantly between sites, zones and seasons (Clarke & Warwick, 1994). ANOSIM is based on a matrix of Bray-Curtis similarities computed for each possible sample pair by comparison of the $\log(x+1)$ -transformed species abundances (averaged across transect sections). Two null hypotheses were tested: (1) there were no significant differences in species composition between sites and intertidal zones (by means of a two-way nested ANOSIM), and (2) there were no differences in species composition between sites and seasons (by means of a two-way crossed ANOSIM). Global tests for differences among any sites, zones or seasons were followed by post-hoc pairwise ANOSIM tests to check between which sites, zones or seasons differences were significant. The P values of post-hoc tests were Bonferroni corrected to account for the enhanced probability of Type I errors in multiple comparisons. Non-metric Multi Dimensional Scaling (MDS) ordination was used to produce 2-d plots which represent the inter-sample resemblances in such a way that the relative distances between points in the plot are measures of their degree of similarity. A stress value indicates how well the sample relationships are represented in the plot (Clarke & Warwick, 1994). Finally, analyses of the species' similarity percentages (SIMPER) were used to identify species which contributed most to the faunistic differences between sites, zones and seasons.

3.3 Results

3.3.1 Temperature and salinity

The seawater temperature varied slightly from 30.3 to 34.8 °C at Arakan, 29.4 to 33.8 °C at Mokupa and 31.4 to 35.8 °C at Likupang (Figure 3.1). The seasonal fluctuations showed almost the same trend at all three sites. Minimum values occurred in January during peak wet season and maximum values during peak dry season in July. The sea water temperatures showed largely the same pattern as the air temperatures (Figure 2.5).

Salinities in tide pools at the different sites did not differ greatly from each other, ranging from 27 to 35 at Arakan, 28 to 35 at Mokupa and 29 to 40 at Likupang (Figure 3.2). Lowest values were always recorded during the wet season in January, while the maximum salinities occurred during peak of dry season in July (Figure 3.2).

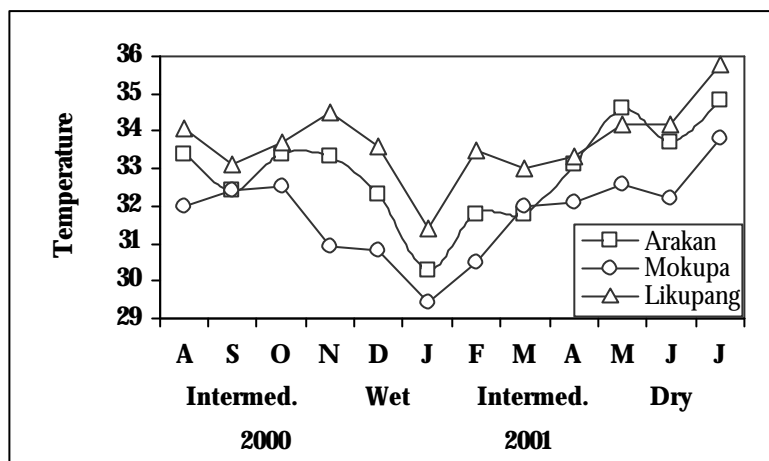


Figure 3.1. Annual variations of sea water temperatures at Arakan, Mokupa and Likupang from August 2000 to July 2001

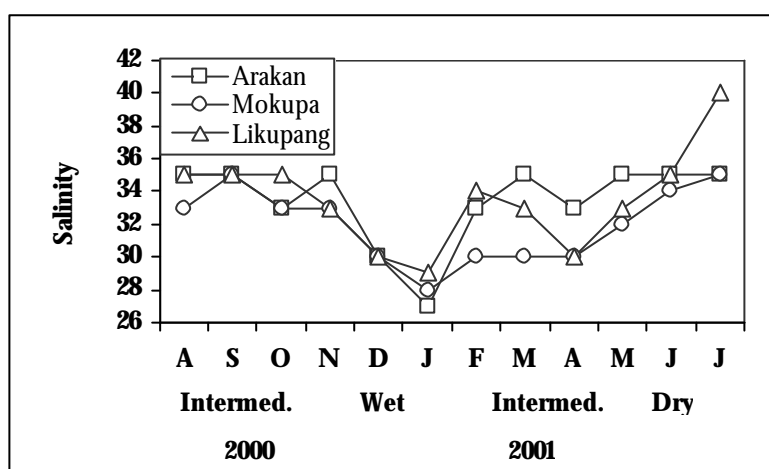


Figure 3.2. Annual variations of salinities at Arakan, Mokupa and Likupang from August 2000 to July 2001

3.3.2 Species composition and description

A total of 8 nassariids species were found at Arakan, Mokupa and Likupang (Table 3.3 and Figure 3.3). Species numbers were highest at Arakan (6), followed by Mokupa (5) and Likupang (4).

Table 3.3. List of species encountered during the sampling period. x = present, * one time present

Species	Arakan	Mokupa	Likupang
<i>Nassarius bimaculosus</i>	x	x	x
<i>Nassarius camellus</i>	x		
<i>Nassarius globosus</i>	x	x	
<i>Nassarius livescens*</i>			x
<i>Nassarius luridus</i>	x	x	
<i>Nassarius pullus</i>	x	x	x
<i>Nassarius venustus</i>			x
<i>Hebra corticata</i>	x	x	x

Three species, *N. bimaculosus*, *N. pullus* and *H. corticata*, were found at each site. Two species (*N. globosus* and *N. luridus*) did occur at both Arakan and Mokupa but were absent at Likupang. Another two species, *N. camellus* and *N. venustus* were only found in one site (Arakan and Likupang respectively), while *N. livescens* only one specimen at Likupang during the study period and its discarded for further analysis.

The identification to species level was principally based on the morphological characteristics described by Cernohorsky (1984) and Wilson (1994). Hugo. H. Kool (Dieren Netherland), re-examined the material collected to confirm proper species identification.

Nassarius (Plicarularia) bimaculosus (Adams, 1852) can be identified by the dark brown spot(s) on the outside of the outer lip: one spot on an adult, two on a juvenile. Shell lengths vary from 6 to 19 mm. This species is commonly seen on the flats of Likupang where sediments consist of sand and coarse sand. Its also often found in tidal pools Arakan.

N. (Plicarularia) camellus (Martens, 1897) It is rather small and received its name because of its pronounced camel-like shell hump, shell lengths vary from 5 to 11 mm. It is rather rare off Northern Minahasa and occurred only in Arakan.

N. (Plicarularia) globosus (Quoy & Gaimard, 1833) its characterised by its thick and smooth outer lip. Shell lengths vary from 7 to 14 mm. This is a very common species on the muddy flats of Arakan and Mokupa where it was always found in close association with *N. pullus*. However, in contrast to the latter species it does not climb on the seagrass leaves.

N. (Telasco) luridus (Gould, 1850) can be recognized by very small light spots distributed all over the surface of the shell. Its body shape is very variable, ranging from slender to bulbish. Shell lengths vary from 7 to 22 mm. This species, was common on the sandy flats of Mokupa and was occasionally also found on the muddy sand flat of Arakan.

N. (Plicarularia) pullus (Linneaus, 1758) is quite similar to *N. bimaculosus* but its grows larger. There is a hump on the back side of this species and it is oddly flat on the right side. The outer lip is most often yellow, sometimes off-white to brownish. Shell lengths vary from 7 to 21 mm. It was very common on the flats of Arakan and was also found at Mokupa and Likupang, albeit in lower abundances. By using its siphon, *N. pullus* can breath even when it is buried in the mud.

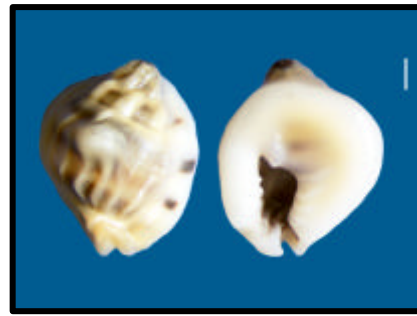
N. (Niotha) venustus (Dunker, 1847) features a peculiar shell sculpture and very thick outer lip. Shell lengths vary from 15 to 20 mm. It was found only on the upper coarse-sandy flats of Likupang.

N. livescens (Philippi, 1849) was found with only one specimen on the coarse sand of Likupang, so that this species was excluded for further analysis. Its shell length was 11 mm.

Hebra corticata (Adams, 1852) only lives on the leaves of the seagrass *E. accoroides*. Shell lengths vary from 7 to 18 mm. It was very common in the intertidal seagrass meadows of Arakan and Mokupa.



Nassarius bimaculosus



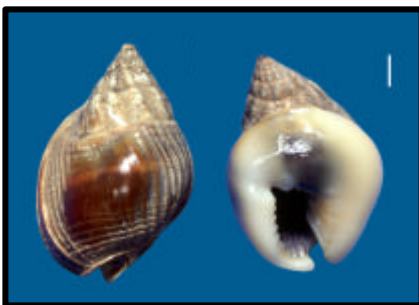
Nassarius camellus



Nassarius globosus



Nassarius luridus



Nassarius pullus



Nassarius venustus



Hebra corticata



Nassarius livescens

Figure 3.3. Nassariid species found on the intertidal mudflats off Northern Minahasa Peninsula, Indonesia. (—) : 1 mm scale

3.3.3 Abundances

Total monthly average densities of nassariid species at the intertidal study sites off northern Minahasa ranged between about 12 ind.m⁻² in the middle zone of Arakan (in August and December) and the upper zone of Mokupa (in January) and < 1 ind m⁻² in the lower zones of Mokupa and Likupang (Figure 3.4).

A 3-way ANOVA indicated that the densities differed significantly among study sites and among intertidal zones (Table 3.4). Post-hoc multiple comparisons of (log-transformed) mean densities indicated:

- 1) Average nassariid densities were different between all three sites, being highest at Arakan, followed by Mokupa and lowest at Likupang (Tukey HSD, $Q = 2.39$, $P < 0.05$).
- 2) Average nassariid densities decreased along the upper-middle-lower tidal gradient. (Tukey HSD, $Q = 3.20$, $P < 0.05$). However, the tidal main effect was confounded to a certain degree by a significant interaction between sites and zones, since at Arakan nassariid snails were most abundant in the middle instead of the upper zone (Table 5).

On average, abundances also differed significantly between seasons (Table 3.4), with the wet season featuring significantly higher densities than all other three seasons (Tukey HSD, $Q = 2.63$, $P < 0.05$). The interaction terms site*season and zone*season indicate that this seasonal pattern was consistent in all three intertidal zones but not at all three sites (Table 3.4).

Table 3.4. Summary of 3-way ANOVA of total monthly nassariid densities (ind m⁻²) off northern Minahasa, Sulawesi, Indonesia. Factors were SITE (Arakan, Mokupa, and Likupang), intertidal ZONE (upper, middle, and lower; nested into SITE) and SEASON (dry, dry-wet intermediate, wet, and wet-dry intermediate). *df* = degree of freedom, *SS* = Sum of Squares, *MS* = Means of Squares. Density values were log($x + 1$)-transformed before analysis.

Source of Variation	df	SS	MS	F	P
Site	2	15.44	7.72	66.02	< 0.0001
Zone[Site]	6	28.24	4.71	40.26	< 0.0001
Season	3	1.77	0.59	5.04	0.0032
Site * Season	6	1.62	0.27	2.31	0.0425
Zone[Site] * Season	18	1.89	0.10	0.90	0.5833
Within	72	8.42	0.12		
Total	107	57.37			

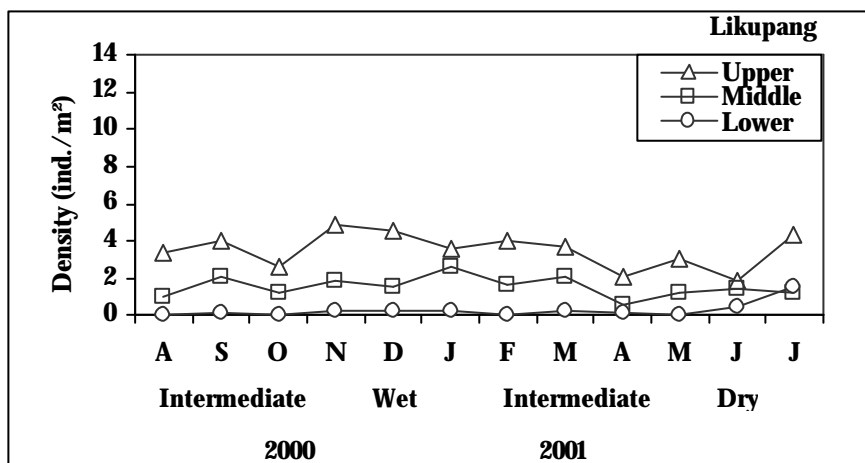
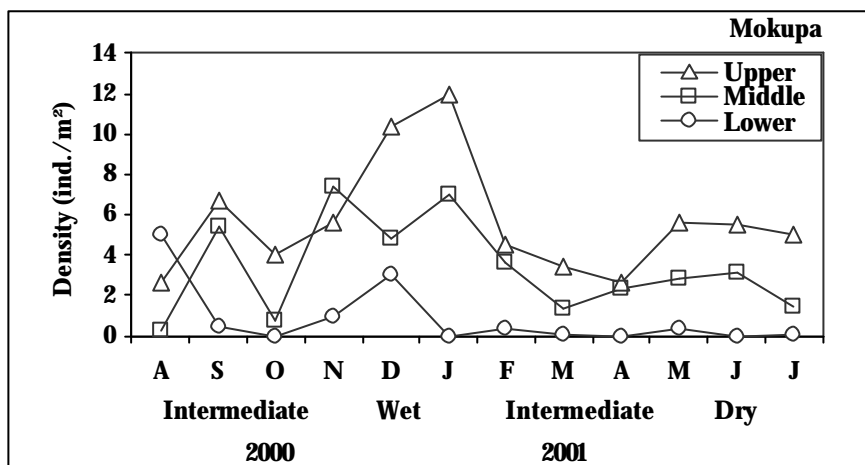
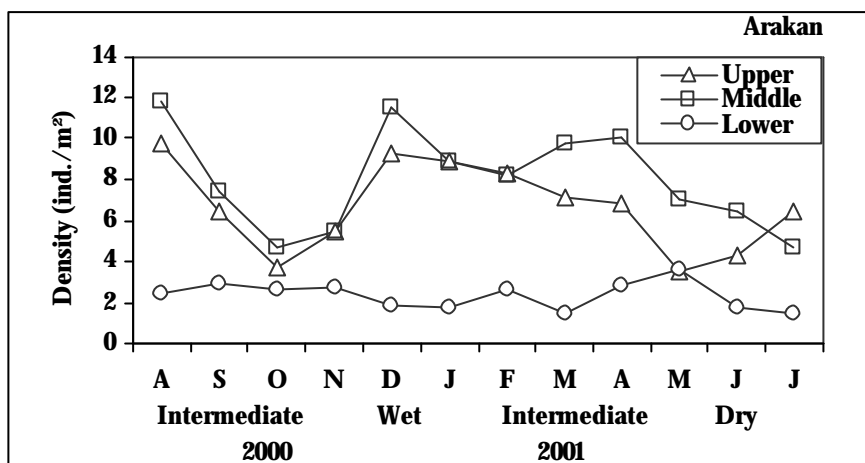


Figure 3.4. Total average monthly densities (ind m²) of nassariid species in three intertidal zones (upper, middle, and lower) at three sites (Arakan, Mokupa, and Likupang) off northern Minahasa, Sulawesi, Indonesia, from August 2000 to July 2001.

Only one nassariid species, *Nassarius pullus*, was found at all three sites and in all tidal zones (Table 3.5). *N. pullus* and *N. globosus*, of which the latter was absent at Likupang, were most abundant in the upper to middle zones of Arakan, together accounting for 81% and 45%, respectively, of the total yearly average densities (Table 3.5, Figure 3.5). Both species exhibited a pronounced decrease of densities from the upper through the middle to the lower zone.

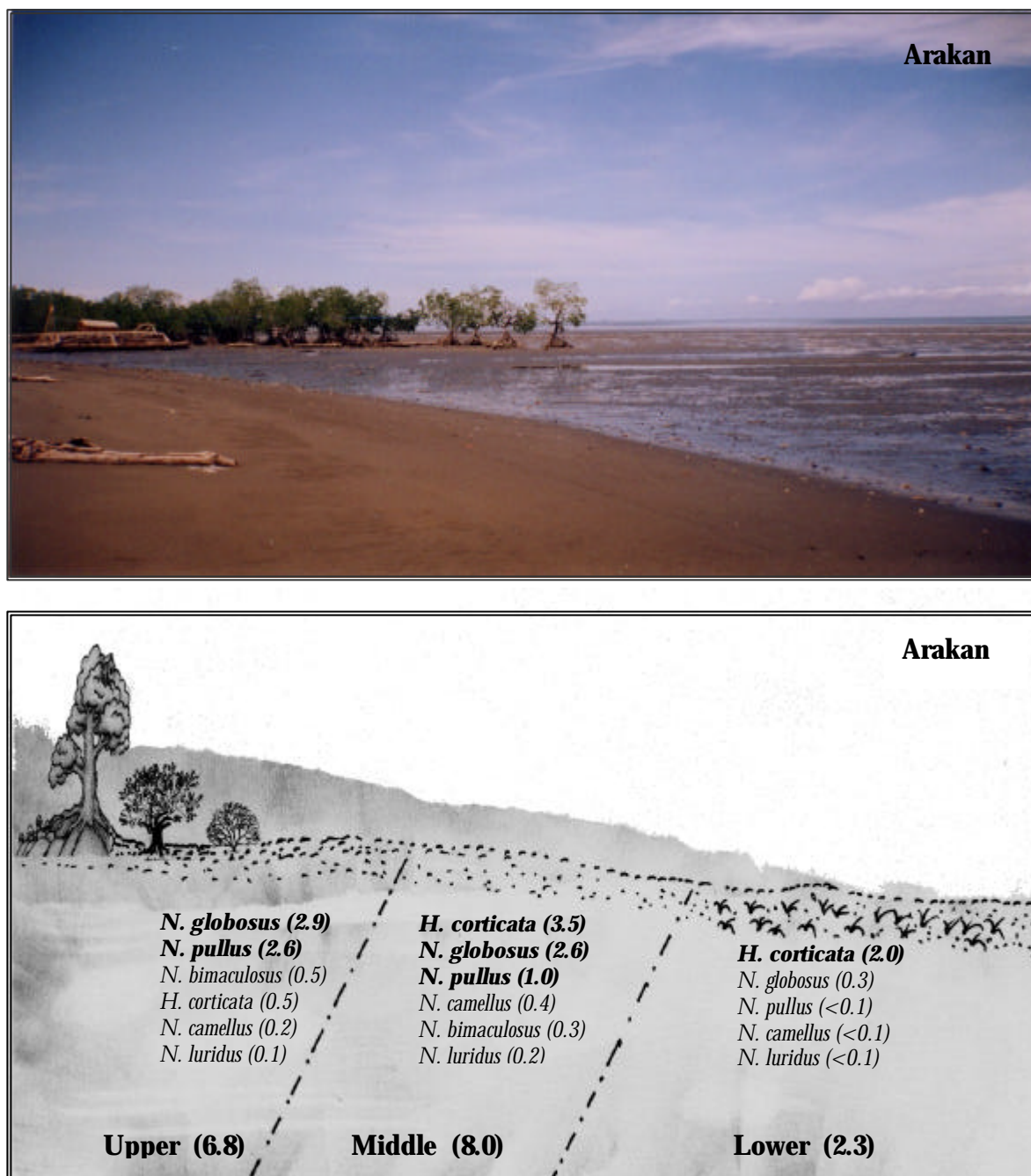


Figure 3.5. Arakan. Intertidal zonation of nassariid fauna. Species listed in descending order of abundances. Dominant species in bold. Numbers in brackets are yearly average densities (ind m⁻²). The distribution of seagrass is indicated.

The seagrass-associated species *H. corticata* dominated the middle and lower zone at Arakan (relative abundances of 44% and 85%, respectively; Table 3.5, Figure 3.5) and all three intertidal zones at Mokupa (relative abundances of 43%, 43%, and 40%; Table 3.5, Figure 3.6).

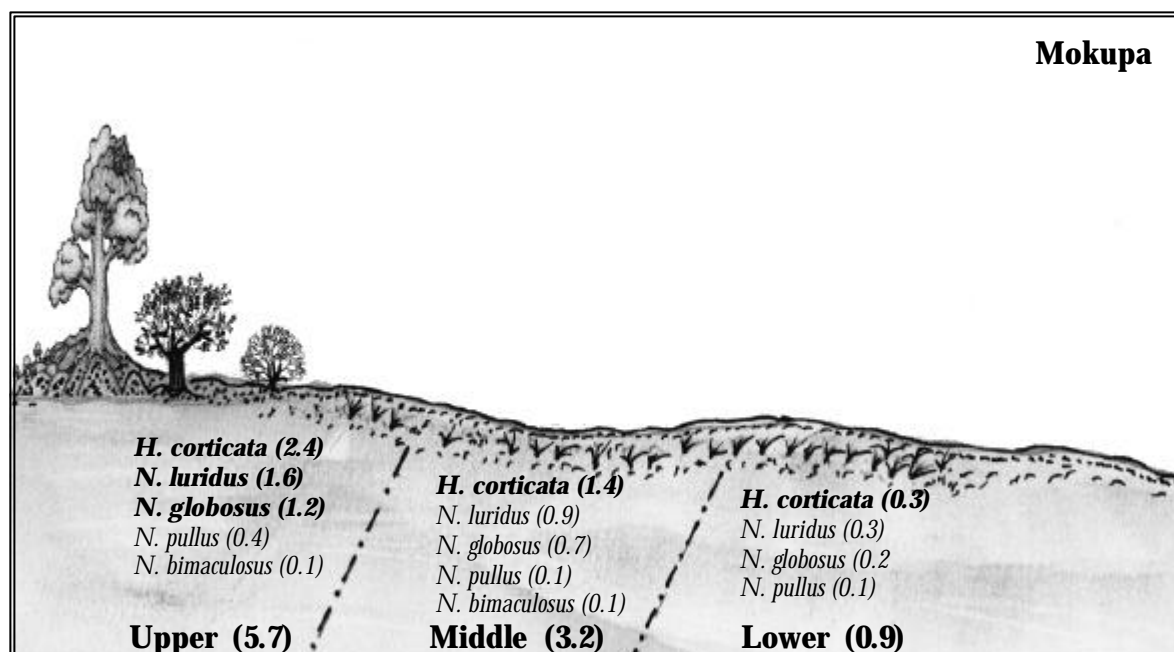


Figure 3.6. Mokupa. Intertidal zonation of nassariid fauna. Species listed in descending order of abundances. Dominant species in bold. Numbers in brackets are yearly average densities (ind m⁻²). The distribution of seagrass is indicated.

At Likupang, the comparatively poor nassariid fauna was dominated by *N. bimaculosus*, which accounted for 80%, 88% and 73% of the total abundances in the upper, middle and lower zone, respectively (Table 3.5, Figure 3.7). This species did also occur at the other two sites, albeit only at low abundances and only in the upper and middle zones.

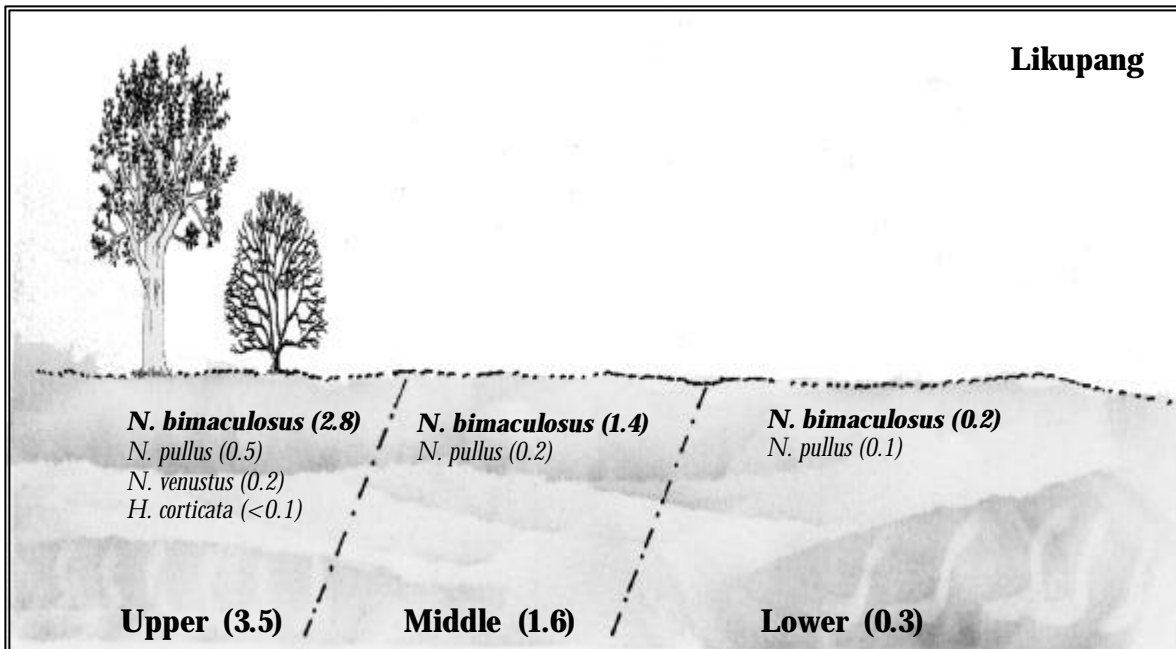


Figure 3.7. Likupang. Intertidal zonation of nassariid fauna. Species listed in descending order of abundances. Dominant species in bold. Numbers in brackets are yearly average densities (ind m⁻²).

Table 3.5. Yearly average densities (ind m⁻²) of seven nassariid species along a tidal gradient at three study sites (Arakan, Mokupa, and Likupang) off northern Minahasa, Sulawesi, Indonesia. u = upper zone, m = middle zone, and l = lower zone. Dominant species in bold.

Species	Arakan			Mokupa			Likupang		
	u	m	l	u	m	l	u	m	l
<i>N. bimaculosus</i>	0.49	0.29	0	0.11	0.09	0	2.80	1.36	0.22
<i>N. camellus</i>	0.20	0.38	0.02	0	0	0	0	0	0
<i>N. globosus</i>	2.86	2.58	0.27	1.19	0.73	0.15	0	0	0
<i>N. luridus</i>	0.11	0.19	0.02	1.55	0.93	0.29	0	0	0
<i>N. pullus</i>	2.56	1.03	0.04	0.39	0.14	0.07	0.48	0.19	0.08
<i>N. venustus</i>	0	0	0	0	0	0	0.19	0	0
<i>H. corticata</i>	0.47	3.53	1.98	2.41	1.44	0.34	0.04	0	0
Total	6.69	8.00	2.33	5.65	3.33	0.85	3.51	1.55	0.30

3.3.4 Biomass

The spatial and temporal nassariid biomass distribution off northern Minahasa exhibited a very similar pattern as the abundances. Total monthly average biomass ranged between > 400 mg AFDW m⁻² in the upper zone of Arakan in February to < 1 mg AFDW m⁻² in the lower zones of all three study sites (Figure 3.8).

A 3-way ANOVA shows that biomass differed significantly among study sites and intertidal zones (Table 3.6). Values were highest at Arakan, followed by Mokupa and Likupang (Tukey post-hoc tests). With regard to the tidal gradient, biomass was highest in the upper zone at all three sites and decreased significantly to the middle and lower zone (Tukey post-hoc tests). The biomass differed also significantly among seasons, being significantly higher during wet than during the other three seasons (Tukey post-hoc tests). The insignificant interaction terms site*season and zone[site]*season indicate that the seasonal pattern was consistent at all three sites and in all three intertidal zones.

Table 3.6. Summary of a 3-way ANOVA of total monthly nassariid biomass (mg AFDW m⁻²) off northern Minahasa, Sulawesi, Indonesia. Factors were SITE (Arakan, Mokupa, and Likupang), intertidal ZONE (upper, middle, and lower; nested into SITE) and SEASON (dry, dry-wet intermediate, wet, and wet-dry intermediate). *df* = degree of freedom, *SS* = Sum of Squares, *MS* = Means of Squares. Density values were $\log(x + 1)$ -transformed before analysis.

Source of Variation	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Site	2	55.95	27.98	31.65	< 0.0001
Zone[Site]	6	194.92	32.49	36.76	< 0.0001
Season	3	10.55	3.52	3.98	0.0111
Site * Season	6	10.31	1.72	1.95	0.0851
Zone[Site] * Season	18	15.29	0.85	0.96	0.5119
Within	72	63.64	0.88		
Total	107	350.67			

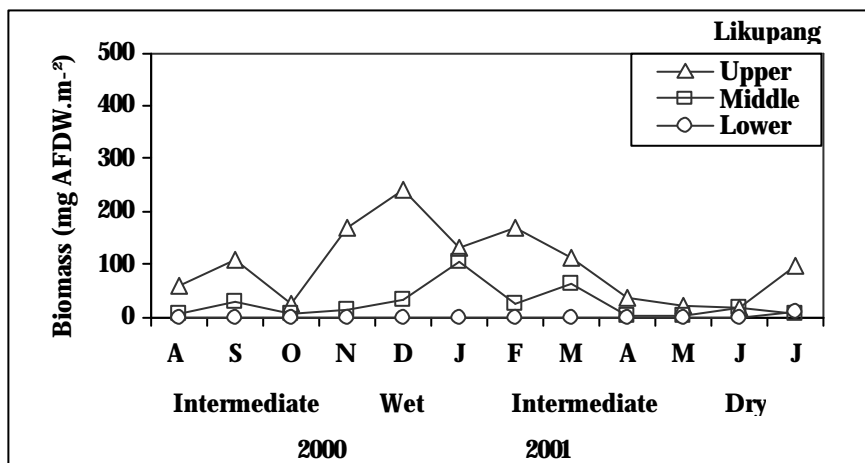
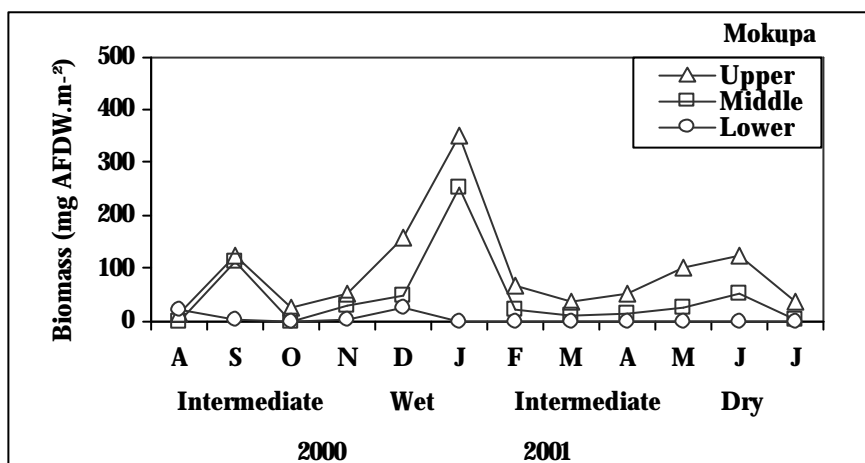
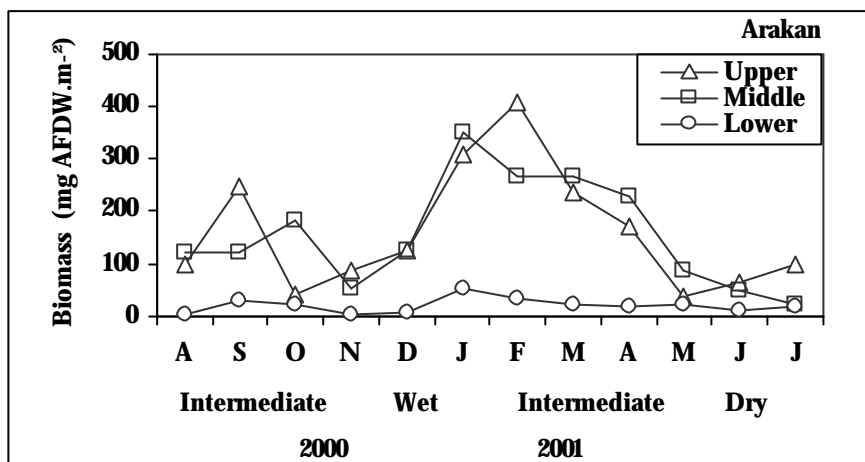


Figure 3.8. Total average monthly biomass (mg AFDW m⁻²) of nassariid species in three intertidal zones (upper, middle, and lower) at three sites (Arakan, Mokupa and Likupang) off northern Minahasa, Sulawesi, Indonesia, from August 2000 to July 2001.

The biomass dominance patterns was largely the same as the abundance dominance pattern (see Table 3.5). In the upper zone of Arakan, *N. pullus* and *N. globosus* clearly dominated the nassariid biomass, together accounting for 97% of the total biomass (Table 3.7). The seagrass-associated species *Hebra corticata*, gained more importance in the middle and lower zones, contributing 57% and 95%, respectively, to the total biomass. At Mokupa, *H. corticata*, *N. luridus* and *N. globosus* clearly dominated the nassariid biomass in all three zones (Table 3.7), while *N. bimaculosus* was most important at Likupang (Table 3.7).

Table 3.7. Yearly average biomass (mg AFDW m⁻²) of seven nassariid species along a tidal gradient at three study sites (Arakan, Mokupa, and Likupang) off northern Minahasa, Sulawesi, Indonesia. u = upper zone, m = middle zone, and l = lower zone. Dominant species in bold.

Species	Arakan			Mokupa			Likupang		
	u	m	l	u	m	l	u	m	l
<i>N. bimaculosus</i>	2.36	0.59	0	0.59	0.29	0	89.95	25.52	1.10
<i>N. camellus</i>	0.44	1.36	0	0	0	0	0	0	0
<i>N. globosus</i>	51.71	42.97	0.99	16.28	6.55	0.17	0	0	0
<i>N. luridus</i>	0.64	1.68	0.01	33.04	16.83	2.44	0	0	0
<i>N. pullus</i>	103.96	20.82	0.06	3.65	0.27	0.23	8.23	0.78	0.35
<i>N. venustus</i>	0	0	0	0	0	0	1.56	0	0
<i>H. corticata</i>	1.76	89.21	18.33	41.67	23.67	1.80	0.11	0	0
Total	160.86	156.63	19.39	95.24	47.60	4.63	99.85	26.30	1.44

3.3.5 Community structure

A 2-way nested ANOSIM (Sites x Zones[Sites]) indicated that there were significant differences in nassariid species composition between study sites (Global R = 0.695, P = 0.004) as well as intertidal zones nested within the sites (Global R = 0.571, P = 0.001). The MDS plot (Figure 3.9) visualizes this pattern. Likupang was clearly disparate from the other locations but also Arakan and Mokupa exhibited only little overlap, illustrating that all sites differed significantly in species composition. The intertidal zonation was clearly pronounced at Likupang and Arakan, albeit the gradients in the multispecies distribution did not run into the same direction. In contrast, the distribution of nassariid snails was more heterogeneous at Mokupa and did not show a clear-cut intertidal pattern.

The faunistic differences between the sites and zones, as illustrated in the MDS plot (Figure 3.9), were primarily determined by pronounced gradients in the distribution of *N. bimaculosus*, *H. corticata* and *N. luridus*, as a correlation analysis between the positions of the samples in the plot (i.e., their x and y coordinates) and the abundances of the nassariid species suggests (Table 3.8).

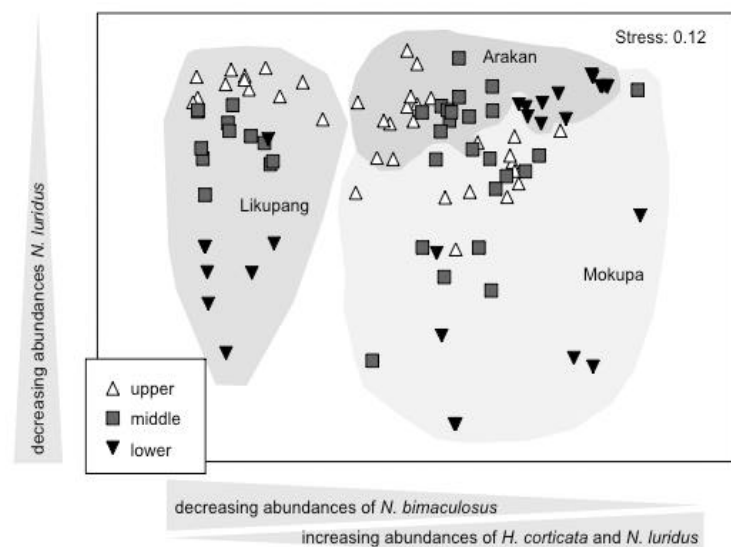


Figure 3.9. MDS plot, illustrating the similarity pattern of nassariid samples taken in three intertidal zones (upper, middle, and lower) at three study sites (Arakan, Mokupa and Likupang) off Northern Minahasa, Sulawesi, Indonesia.

Table 3.8. Spearman rank correlations between nassariid species abundances in the samples and MDS plot coordinates (x axis, y axis). Significance levels are Bonferroni corrected. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

Species	MDS x axis	MDS y axis
<i>N. bimaculosus</i>	- 0.840***	0.305*
<i>N. camellus</i>	0.064	0.230
<i>N. globosus</i>	0.313*	0.029
<i>N. luridus</i>	0.414***	- 0.462***
<i>N. pullus</i>	- 0.145	0.310*
<i>N. venustus</i>	- 0.317*	0.353**
<i>H. corticata</i>	0.712***	0.227

In contrast to the distinct spatial patterns at different scales (sites, zones), there was no clear seasonal trend in the temporal dynamics of the nassariid assemblages, as a one-way ANOSIM test looking at differences in species composition between the dry, wet and the intermediate seasons (Global $R = 0.004$, $P = 0.334$) as well as the essentially arbitrary distribution of samples in the MDS plot (Figure 3.10) indicate.

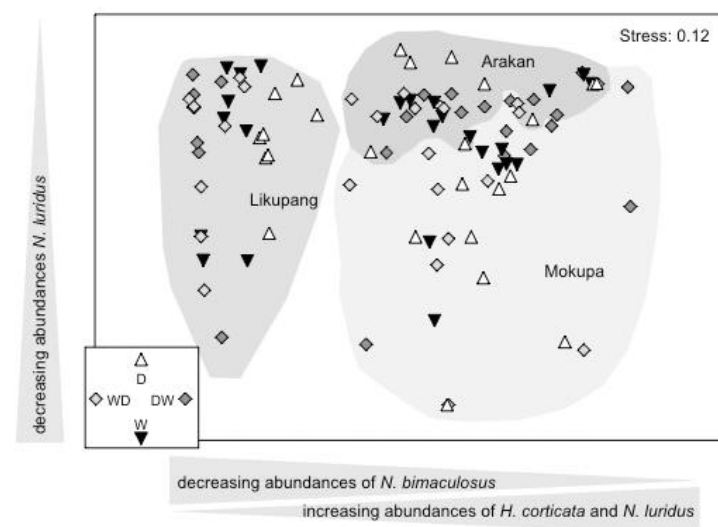


Figure 3.10. MDS plot, illustrating the similarity pattern of nassariid samples taken at three study sites (Arakan, Likupang, and Mokupa) off Northern Minahasa, Sulawesi, Indonesia during four seasons (D: dry; DW: dry-wet intermediate; W: wet; and WD: wet-dry intermediate) between August 2000 and July 2001.

3.4 Discussion

3.4.1 Species composition

Taxonomically the family Nassariidae is close to the Buccinidae, and according to some authors it even has the status of a sub-family (Nassariinae) within the Buccinidae (e.g., Wilson, 1994). Others, e.g., Cernohorsky (1984), argue that the differences in radular dentition, foot morphology as well as shell and operculum features justify the erection of a separate family. For species identification, I used the keys provided by Cernohorsky (1984) who reported a total of 211 nassariid species to occur in the tropical Indo-Pacific, a number which is three times higher than those recorded in the other biogeographic regions.

In total, I found eight nassariid species at the tidal flats off the coasts of Northern Minahasa (Sulawesi, Indonesia). In other study areas in both tropical and temperate regions, the number of nassariids was clearly lower (Table 3.9). However, this finding should be interpreted with care. In general, comparisons between different investigations are problematic because discrepancies in the methods used (e.g., number and spatio-temporal distribution of samples, taxonomic determination level) can easily obscure real diversity differences (Dittmann, 1995; Pepping et al., 1997).

Kool and Strack (2000) collected a total of 47 species in the waters off Ambon. However, in contrast to my investigation their study was a faunistic survey that specifically aimed at a comprehensive inventory of the regional species diversity, which involved a large number of samples in order to assess the species pool of a larger area comprising a variety of different marine habitats. Their list includes the eight intertidal species I found. It is, thus, very likely that additional nassariid species occur off northern Minahasa in subtidal habitats that were not investigated during my study.

3.4.2 Spatial patterns

Both abundance and biomass of the nassariid fauna off northern Minahasa varied significantly between study sites and intertidal zones. In general, they decreased along the tidal gradient from the upper to the lower zone. Only at Arakan, abundances were highest in the middle zone, whereas average body size and, hence, biomass were also highest in the upper zone. This zonation pattern was evident despite a pronounced small-scale (i.e., within-zone) patchiness in the distribution of nassariid snails.

Table 3.9. Nassariid species reported from temperate and tropical intertidal sites. na: not available, DW: Dry Weight, WW: Wet Weight, AFDW: Ash Free Dry Weight, * Sungei Buloh, ** Kuala Selangor

Location	Habitat	Species	Density (ind. m ⁻²)	Biomass (gr m ⁻²)	Source
Temperate areas:					
Buzzards Bay, USA Barnstable, Harbor,	Mudflat	<i>N. triviattatus</i>	45	0.17 DW	Sanders, 1958
Massachusetts, USA	Mudflat	<i>N. obsoletus</i>	209	18.89 DW	Sanders et al., 1962
Gulf of California	Mudflat	<i>N. tiarula</i>	na	na	Houston, 1971
Massachusetts, USA	Mudflat	<i>N. obsoletus</i>	na	na	Whitlatch, 1977
Lake Grevelingen, Netherlands	Sheltered places	<i>N. reticulatus</i>	2 – 7	0.02 – 4.99 AFDW	Lambeck, 1984
South Australia	Sandflat	<i>N. pauperatus</i>	na	na	McKillup et al., 1993
Leschenault Inlet estuary, Western Australia	Muddy sand, Mud	<i>N. burcharidi</i> <i>N. nigellus</i>	3.2 – 400 na	na na	Semeniuk & Wurm, 2000
Galicia, NW Spain	Mud and sand	<i>N. reticulatus</i>	na	na	Barreiro et al., 2001
South-eastern USA	Mudflat	<i>N. vibex</i>	na	na	Demaintenon, 2001a
Tropical areas:					
Kampong Mata Ikan, Singapore	Sandflat	<i>N. costatus</i>	7	na	Vohra, 1971
		<i>N. jacksonianus</i>	240	na	
		<i>N. muricatus</i>	28	na	
	Mangroves	<i>N. thersites</i>	15	na	
		<i>N. hepaticus</i>	na	na	
		<i>N. thersites</i>	na	na	
Rock, debris and wood	<i>N. olivaceus</i>	na	na		
Kingston Harbour, Jamaica	Sandflat	<i>Nassarius sp.</i>	10	na	Wade, 1972
Sungei Buloh and Kuala Selangor, Malaysia	Mudflat	<i>Plicarularia</i>	31.5 *	3.85 WW*	Broom, 1982
		<i>leptospira</i>	70 **	9.75 WW**	
		<i>P. pulla</i>	0.95 *	0.4 WW*	
		(= <i>N. pullus</i>)	3.25 **	2.85 WW **	
		<i>N. jacksonianus</i>	0.45 *	0.18 WW *	
			1.13 **	0.78 WW**	
		<i>N. planocostata</i>	0.15*	0.08 WW*	
		<i>N. maculosa</i>	0.4 **	0.23 WW**	
		4	55 WW		
Roebuck Bay, Western Australia	Muddy sand	<i>N. dorsatus</i>	na	na	Pepping et al., 1997
		<i>Nassarius sp1.</i>	na	na	
		<i>Nassarius sp2.</i>	na	na	
Hila Ambon, Indonesia	Sand	<i>N. conoidalis</i>	1	na	Kohn, 1998
		<i>N. crenoliratus</i>	2	na	
		<i>Nassarius sp.</i>	1	na	
Subang, West Java, Indonesia	Muddy sand	<i>N. pussila</i>	2.3 – 4	na	Omar & Yulianda, 2000
Haughton River estuary, Queensland, Australia	Muddy sand	<i>Nassarius spp.</i>	na	na	Dittmann & Vargas, 2001

Comparisons of between tropical and temperate intertidal assemblages mostly suggest that species diversities are generally higher and abundances generally lower in tropical than in temperate wadden areas (Dittmann & Vargas, 1991; Reise, 1991). However, according to the review of Alongi (1990) the densities of tropical intertidal soft-bottom communities do not differ significantly from their temperate counterparts. With regard to the nassariids, my results and those compiled in Table 3.9 rather corroborate the former notion of comparatively low intertidal abundances in the tropics. Although the values vary widely among temperate and tropical study sites (and such comparison should generally be interpreted with due care as they are easily confounded by methodological bias due to differences in sampling methods, habitats, seasons etc.), there is a trend that the nassariid densities reported from temperate wadden areas are up to one order of magnitude higher than those recorded at tropical flats (Table 3.9).

It is well known that the distribution of intertidal organisms – in both temperate and tropical regions – is affected by a wide variety of environmental parameters, such as bottom topography, sediment composition, wave disturbance, tidal characteristics and other related factors (Sanders, 1958; Sanders et al., 1962; Vohra, 1971; Broom, 1982; Alongi, 1989, 1990; Dittmann, 1995, 2000). However, it is generally difficult to deduce the prime determinants of abundance, biomass and distribution of organisms in a particular environment by comparison of various study sites, even if these sites apparently represent the same habitat, because they will always differ in sedimentological, climatological and hydrographical aspects at a range of spatial and temporal scales. All three intertidal sampling sites off northern Minahasa feature some estuarine characteristics due to riverine input, although the salinities always remained at marine levels throughout the study year.

Likupang is distinguished from Arakan and Mokupa by a clearly higher sediment instability, which is certainly a major stress factor for the intertidal fauna. Hence, only the opportunistic species *N. bimaculosus*, which can cope with the unstable conditions of sandy habitats, occurred throughout the year at Likupang. Other species, *N. pullus* and *N. venustus*, were markedly less frequent.

In contrast, the flats at Arakan primarily consist of finer sediments. The upper and middle zone is characterized by sand and muddy sands, whereas the lower zone features muddy grounds and abundant seagrass meadows (*Enhallus accoroides*). In general, Arakan is a physically more stable environment than Likupang, due to the sheltered nature of the inshore boundary of rough reef limestone, and houses a more diverse and abundant nassariid fauna. Another positive factor may be the continuity in food supply due to the import of riverine organic matter. The nassariid fauna of both the upper and middle zone was dominated by *N. globosus* and *N. pullus*, while the lower assemblage was characterized by the opportunistic seagrass-associated *H. corticata*.

Mokupa is characterised by sandy – and, hence, less stable – substrates as well as poorer seagrass cover. Nevertheless, it also featured three to five nassariid species which, however,

reached lower densities and biomass than at Arakan. The between-zone differences in species composition were not as pronounced as at Arakan, as *H. corticata* and *N. globosus* dominated throughout the entire tidal gradient, particularly at upper to middle zones.

In conclusion, contrasting Likupang, Mokupa and Arakan, it is reasonably clear that nassariid densities were generally higher in sheltered muddy habitats than at exposed sandy beaches. Such a pattern has been detected in many benthic investigations (Alongi, 1990).

Findings from field studies on nassariids in temperate regions suggest that the littoral zonation is strongly related to intertidal migration patterns, which are related to spatial and/or temporal variations in salinity, sediment composition and food availability. Barnett et al. (1980) reported that *N. reticulatus* reaches highest densities at and below the spring-tide low-water mark at sheltered sandy shores in Britain. However, this general distribution pattern is overlaid by a patchiness at a smaller scale caused by migration to suitable places for egg-capsule deposition, particularly if such places are in shortage. Feeding migrations may also lead to random small-scale patchiness. Crisp (1978) reported that *Nassarius* specimens actively move upstream towards food over distances of up to several metres. In Kvarnbukten Bay, Sweden, *N. reticulatus* lives primarily in eel-grass meadows at the low-water mark during summer but wanders offshore during winter (Tallmark, 1980). The American estuarine species *N. obsoletus* moves in spring from subtidal waters to intertidal flats where it prefers muddy grounds but is occasionally also found in tidal pools and salt marshes (Brenchley, 1980; Smith, 1980). In the Leschenault Inlet, western Australia, the common estuarine species *N. burchardi* reaches highest densities at subtidal depths in middle to lower-estuarine habitats, while juvenile specimens of the stenohaline marine species *N. nigellus*, probably originating from outside the inlet, are largely confined to the lower-estuarine inlet basin (Semeniuk & Wurm, 2000).

For tropical nassariids less information on abundances, biomass and distribution is available, and the results imply that there is not a consistent pattern. At Kampong Mata Ikan (Singapore), *N. jacksonianus* is present along the entire intertidal sand-mud gradient but reaches highest abundances at lower-zone muddy grounds, just as the less frequent *N. muricatus* and *N. costatus* (Vohra, 1971). Unlike these species, *N. thersites* and *N. olivaceus* obviously prefer the upper-zone mangrove swamps. In addition, Vohra (1971) reported that the biggest nassariid specimens occurred in the upper zone, probably because of an ontogenetic up-shore migration as well as more favourable environmental and feeding conditions. McLachlan & Jamarillo (1995) claimed that up-shore migrations are advantageous because they keep the snails out of reach of aquatic predators and at the same time result in an improved access to good food sources. Pepping et al. (1997) reported that *N. dorsatus* is most abundant on silty substrates between the upper and middle zone in Roebuck Bay, western Australia. In the Haughton River estuary, NE Australia, *Nassarius* spp. had highest densities in the middle intertidal zone (Dittmann, 2000; Dittmann & Vargas, 2001). In contrast, Broom (1982) did not detect any particular zonation pattern in the distribution of nassariid snails at Malaysian intertidal mudflats. He suggested that

this might be explained by the fact that *N. maculosa* propagates by internal fertilization and, hence, its reproduction is independent from environmental factors.

There has been much discussion in the literature concerning the significance of food availability in determining feeding types and zonation of intertidal nassariids. Trophic mode segregation has been well documented (Sanders, 1958; Sanders et al., 1962; Crisp, 1978; Broom, 1982; Cernohorsky, 1984; Britton & Morton, 1994; Pepping et al., 1997; Morton & Yuen, 2000). Most nassariids are carnivores or scavengers, consuming both plant and animal material. The dominance of these feeding modes is typical of gently sloping sand beaches experiencing moderate wave action, a moderate to large tidal amplitude and slowly receding tides. The nassariid species that were preferably found in the upper and middle zones at Arakan and Mokupa are well known as opportunistic predators and/or scavengers. However, some nassariid species are non-selective deposit feeders, which is the characteristic feeding type of fine-sediment habitats (Sanders et al., 1962). The seagrass meadows or patches, primarily occurring on muddy grounds of the middle and lower zones, were preferably colonized by *H. corticata* and, at markedly lower abundances, *N. globosus*. It is known that dense seagrass cover offers not only shelter for the associated fauna but also provides access to good food supplies. Both *H. corticata*, which primarily lives among or on the seagrass leaves, and *N. globosus*, which was found on the muddy seabed between the seagrass tussocks, were never observed to prey on live animals or feed on carcasses. Therefore, both species are assumed to be deposit feeders that utilize the abundant detritus covering the seagrass leaves and the fine sediments in the seagrass meadows. *N. bimaculosus* strongly dominated the nassariid fauna of the sandy flats at Likupang, particularly in the upper zone where it reached highest abundances and biomass. It is an opportunistic scavenger which is obviously well adapted to the peculiar tidal and sedimentological conditions at Likupang. In ripple marks, which are a characteristic feature of the exposed upper-zone flats during ebb tide, *N. bimaculosus* was only found when feeding on carcasses that got stuck between the marks. Otherwise, the specimens had a closed operculum, thus surviving the ebb tide in a non-feeding state. According to Morton (1994), nassariid scavengers are able to move rapidly to their food items and consume large food quantities (up to 50 to 60% of their wet body mass), which provide sufficient energy for approximately 20 days (Cheung, 1994; Morton & Chan, 1999).

Dittmann (2000) pointed out that the distribution of benthic animals are always affected by both environmental parameters and biotic interactions, irrespective of latitude. Hence, the general zonation does not differ much between temperate and tropical intertidal habitats. Not surprisingly, the distribution patterns of intertidal nassariids off the Minahasa Peninsula are thus in good agreement with those reported from other tropical and temperate tidal flats (Vohra, 1971; Barnett et al., 1980; Brenchley, 1980; Smith, 1980; Tallmark, 1980; Broom, 1982; Pepping et al., 1997; Dittmann, 2000; Dittmann & Vargas, 2001).

3.4.3 Temporal patterns

The temporal variation in abundance, biomass and species composition throughout the study year was markedly less pronounced than the spatial patchiness, i.e. the differences between sites and zones. At Arakan and Mokupa, both abundances and biomass were enhanced during the wet season, whereas at Likupang such an increase was not detected. Furthermore, there was no clear seasonal trend in the variation of the composition of the species assemblages at any site and in any zone. There are four species recorded throughout the year, whereas *N. bimaculosus* only occurred from February to May at Mokupa, *N. camellus* was recorded only during April to July at Arakan, and *N. venustus* was only collected during August, November to January and March to April at Likupang. These three less abundant species may have specific responses to the seasonal variation of environmental conditions, which are presumably related to reproduction (Broom, 1982).

What are the possible reasons for the higher abundance and biomass of nassariids snails at Arakan and Mokupa during the wet season? One reason may be that enhanced terrestrial run-offs cause higher supply of organic matter, positively affecting the abundance and biomass of all benthic animals, including nassariid snails (Beukema & Cadée 1997). Another one could be a seasonal response of nassariids to enhanced physical stress during the dry season. Mean abundance and biomass decreased during the dry-wet intermediate (August to October) at Arakan, probably due to unusually rough weather conditions, but showed no clear trend at Mokupa and Likupang. This finding is rather difficult to be explained because of the lack of environmental information.

In general, key environmental variables that change throughout the year (temperature, salinity) are known to have an important effect on the condition of nassariids and to influence their behaviour and reproductive status. In case there is evidence for seasonality, it may be interpreted as synchronization of reproduction to ensure sufficient food supply for the offspring (Broom, 1982). However, tropical intertidal nassariids enjoy a relatively constant food supply because their habitats are typically extremely rich in organic material. Therefore, a marked seasonal variation in reproduction and abundance cannot be expected (Broom, 1982). However, long-term studies and knowledge of recruitment patterns are needed to test this assumption.

Chapter 4

POPULATION DYNAMICS

4.1 Introduction

In the previous chapter 3 presented results on intertidal nassariid snails off Northern Minahasa at the community level. Here, I will look closer on the autecology of two species, *N. pullus* and *N. bimaculosus*. At Arakan and Likupang, these species reached abundances that were high enough to carry out studies on their population dynamics.

There have been several autoecological studies on the natural history and/or population dynamics of nassariid species in temperate regions. For example, Scheltema (1961, 1964, 1965, 1967) investigated reproduction, feeding habits, growth, and the larval development of *N. obsoletus* in relation to environmental factors. Tallmark (1980) and Lambeck (1984) reviewed the knowledge on distribution and migration patterns, as well as recruitment, mortality and longevity of *N. reticulatus*.

In contrast, there is only scarce information on the population dynamics of tropical species, and nothing is known in this regard about the nassariids off Northern Minahasa. Therefore, I investigated the variations of the population structure of the two above-mentioned abundant species at Arakan and Likupang throughout the one-year study period to estimate growth and mortality rates, determine recruitment patterns and assess the longevity.

4.2 Material and methods

4.2.1 Sampling and size measurements

For the study on population dynamics, I used the same specimens that were collected each month between August 2000 and July 2001 to assess the temporal and spatial distribution patterns (see chapter 3.2). In case the numbers were too small because of low abundance, I continued the sampling process until at least 30 specimens were available. All collected individuals were preserved in a buffered 4% sea water-formalin solution for further analyses.

In the laboratory, the shell lengths of a total of 655 and 962 specimens of *N. pullus* and *N. bimaculosus*, respectively, were measured from the apex to the anterior end of the lip to the nearest 0.1 mm-below using a vernier calliper (Table 4.1).

Table 4.1. Number of individuals of *Nassarius pullus* from Arakan and *N. bimaculosus* from Likupang, which were used on population dynamics studies.

Sampling Date at Arakan	No. of <i>N.pullus</i>	Sampling Date at Likupang	No. of <i>N.bimaculosus</i>
15 August 2000 (11:00 AM)	64	16 August 2000 (11:00 AM)	75
12 September 2000 (11:00 AM)	50	13 September 2000 (11:00 AM)	109
12 October 2000 (11:00 AM)	39	13 October 2000 (11:00 AM)	68
12 November 2000 (11:00 AM)	45	13 November 2000 (11:00 AM)	103
12 December 2000 (11:00 AM)	76	13 December 2000 (11:00 AM)	105
11 January 2001 (11:00 AM)	62	12 January 2001 (12:00 AM)	96
11 February 2001 (12:00 AM)	81	12 February 2001 (13:00 AM)	93
10 March 2001 (11:00 AM)	46	11 March 2001 (11:00 AM)	100
08 April 2001 (10:00 AM)	58	09 April 2001 (12:00 AM)	50
05 May 2001 (10:00 AM)	35	06 May 2001 (10:00 AM)	43
06 June 2001 (11:00 AM)	53	07 June 2001 (11:00 AM)	40
05 July 2001 (11:00 AM)	46	06 July 2001 (11:00 AM)	80

4.2.2 Growth

For each month, size frequency histograms (1 mm-classes) were constructed for both *N. pullus* and *N. bimaculosus*. The time series of monthly size histograms were analysed with the 'Modal class Progression Analysis' (MPA) and the 'Electronic Length Frequency Analysis' (ELEFAN I) implemented in the FISAT (FAO-ICLARM Stock Assessment Tools) software package (Gayanilo et al, 2002).

Using two approaches (Bhattacharya's method (Bhattacharya, 1967) and NORMSEP), MPA identifies first the modes in each histogram and decomposes polymodal size distributions into their normally distributed components. These components, each with a different mean size, are regarded to represent distinct cohorts or age groups that make up the population under study. Then, the progression of the mean size of each identified component is tracked through time, i.e. through the consecutive histograms. Growth, i.e. the increment of body size with age, can finally be estimated by fitting a growth model to the increase of the cohorts' mean sizes with (relative) age.

The von Bertalanffy Growth (VBG) model was used to describe the growth of the nassariid specimens:

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)} \right]$$

where L_t is the shell length at age t , L_∞ the asymptotic length (i.e., the theoretical maximum shell length), K the growth coefficient (parameterizing the rate of growth, i.e. the slope of the growth

curve), and t_0 the theoretical age at length 0 (determining the start of the growth of a settled larvae, i.e. the intercept of the growth curve). This formula has been widely used to express the growth of fish but has frequently been shown to be also applicable to invertebrate animals with hard shells or skeletons, such as crustaceans and molluscs (Sparre & Venema, 1998).

ELEFAN I was used to fit the parameter L_∞ and K of the VBG model to the actual size data (for details see Gayanilo et al, 2002). The third parameter, t_0 , was computed according to Lopez (1979):

$$t_0 = \frac{1}{K} \ln \left[\frac{L_\infty - L_c}{L_\infty} \right]$$

where K and L_∞ are the other two VBA growth parameters and L_c is the length at $t = 0$, i.e. the average length of recruits. In this study, L_c was set to 2 mm, which is a typical shell length of recruits in natural nassariid populations (Lambeck, 1984; McKillup et al, 1993).

4.2.3 Recruitment patterns

FISAT was also used to determine temporal recruitment patterns of *N. pullus* and *N. bimaculosus*. By combining the time-series length-frequency data and the VBG growth parameters, the monthly proportions of recruits (i.e., the smallest size class used in the histograms: 6 mm-below), relative to the total number of recruits within one year, were estimated. If possible, the monthly recruitment pattern can be decomposed into up to two normal components, using the NORMSEP module of FISAT, in order to identify the number and relative strength of recruitment pulses within a year. The basic assumptions underlying this approach are: (1) all individuals in the samples grow as described by the VBG model, and (2) there is zero recruitment in one out of twelve months.

4.2.4 Mortality

Besides by the (constructive) factor 'recruitment', the dynamics of a population is determined by the (destructive) factor 'mortality', i.e. the number of individuals that die within a given period of time. Most commonly, it is expressed as the 'instantaneous rate of mortality' Z in the single negative exponential mortality model (Brey, 2003):

$$N_t = N_0 e^{-Zt}$$

where N_t is the number of individuals of a cohort at (relative) age t , N_0 the number of individuals at (relative) age 0, and t the relative age (which is usually related to one year). Z is assumed to remain constant throughout the whole lifespan of a cohort. The percentage (P) of individuals of a cohort which die within a given period of time t (e.g. one year) can be computed from:

$$P = 100(1 - e^{-Zt})$$

The 'length-converted catch curve' (LCCC) module of FISAT was used to estimate Z . The LCCC approach uses the information about the non-linear individual growth, provided by the VBG formula, to convert the body sizes of the observed length-frequency distributions into relative ages (by accounting for the fact that it takes increasingly longer for an individual to grow through a size class the older the individual gets). Then, the decrease of log-transformed numbers of individuals with relative age in the descending right arm of the LCCC can be expressed by a negative linear regression, the slope of which equals Z (for more details see Sparre & Venema, 1998). The points belonging to the descending right arm of the LCCC are regarded to represent age classes that are (1) fully recruited to the population and (2) fully susceptible to sampling. Younger specimens, i.e. those representing the ascending left arm of the LCCC, are not considered in the computation of Z .

According to Allen (1971), the mortality rate Z is equal to the production-to-biomass ratio P/B of a population provided that (i) the population is in a steady state, (ii) growth can be described by the von Bertalanffy growth model, and (iii) mortality can be described by the single negative exponential mortality model.

4.2.5 Longevity

The longevity, i.e. the natural life span, is defined as the age at which 99% of the individuals of a cohort have died, if exposed to natural mortality only (Pauly, 1982). It is difficult to assess if the investigated specimens cannot be aged directly and if it is not clear whether the population under study is exploited or not (i.e., whether there is a fishing mortality in addition to the natural mortality). However, in case the length of the largest specimen found in a survey is $L_{\max} = 0.95 L_{\infty}$, the longevity can be estimated by $3/K$ (Taylor, 1965), where K is the growth coefficient of the von Bertalanffy growth formula.

4.3 Results

4.3.1 Growth

Figure 4.1 shows the monthly size histograms (August 2000 – July 2001) that were used to estimate the growth parameters of *N. pullus*. Throughout the study year, quite large individuals (= 16 mm-below) numerically dominated the samples and formed a very pronounced stationary mode at 18 mm-below. Other modes at smaller sizes, indicating younger cohorts, were markedly smaller, in some months they were even absent. Lines describe the growth of cohorts identified by ELEFAN.

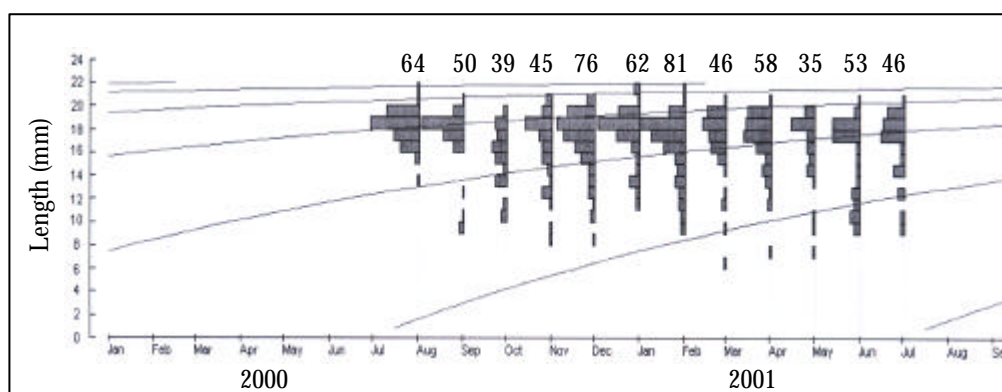


Figure 4.1. *N. pullus*. Size frequency distributions for each month between August 2000 and July 2001, which were used by ELEFAN I to estimate the parameters K and L_{∞} of the von Bertalanffy growth formula. The numbers above the histograms indicate the species sizes. Lines describe the growth of cohorts identified by ELEFAN.

In case of *N. bimaculosus*, a more dynamic development was discernible in the time series of size histograms used for the estimation of growth parameters (Figure 4.2).

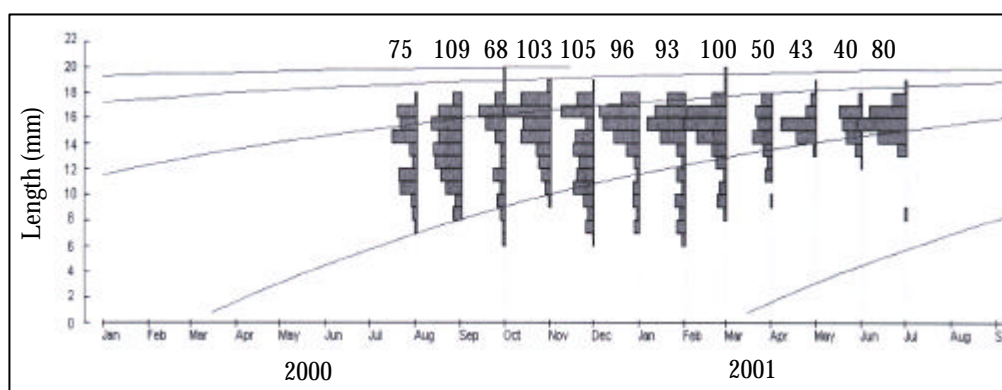


Figure 4.2. *N. bimaculosus*. Size frequency distributions for each month between August 2000 and July 2001, which were used by ELEFAN I to estimate the parameters K and L_{∞} of the von Bertalanffy growth formula. The numbers above the histograms indicate the sample sizes. Lines describe the growth of cohorts identified by ELEFAN.

The mode representing the oldest and largest animals in the samples was not as pronounced and not as stationary as for *N. pullus*, and it was located at markedly smaller lengths (14 to 16 mm-below vs. 17 to 18 mm-below). Minor modes at smaller sizes were discernible in most months and could account for a considerable part of the sample. In comparison to *N. pullus*, *N. bimaculosus* obviously reaches a smaller maximum length, and the population comprised more smaller (and younger) individuals.

The von Bertalanffy growth (VBG) parameters describing the individual growth were $L_{\infty} = 22.6$ mm, $K = 0.78$ year⁻¹ and $t_0 = -0.12$ year for *N. pullus*, and $L_{\infty} = 20.5$ mm, $K = 1.00$ year⁻¹ and $t_0 = -0.10$ year for *N. bimaculosus* (Table 4.2).

Table 4.2. Parameters of the von Bertalanffy growth (VBG) model used to describe the individual growth of *N. pullus* from Arakan and *N. bimaculosus* from Likupang. L_{∞} : asymptotic length (theoretical maximum shell length), K : growth coefficient parameterizing the rate of growth, t_0 : theoretical age at length 0.

Parameters	<i>N. pullus</i>	<i>N. bimaculosus</i>
L_{∞}	22.6 mm	20.5 mm
K	0.78 year ⁻¹	1 year ⁻¹
t_0	- 0.12	- 0.10

Hence, the individual growth of *N. pullus* (Figure 4.3) can be described by the equation $L_t = 22.6 \text{ mm} [1 - e^{-0.78(t+0.12)}]$ and that of *N. bimaculosus* by $L_t = 20.5 \text{ mm} [1 - e^{-1.00(t+0.10)}]$ (Figure 4.4). These results imply that individuals of *N. pullus* grow more slowly than those of *N. bimaculosus* (0.78 year⁻¹ vs. 1.00 year⁻¹) but can get bigger (22.6 mm vs. 20.5 mm) if they reach their maximum age.

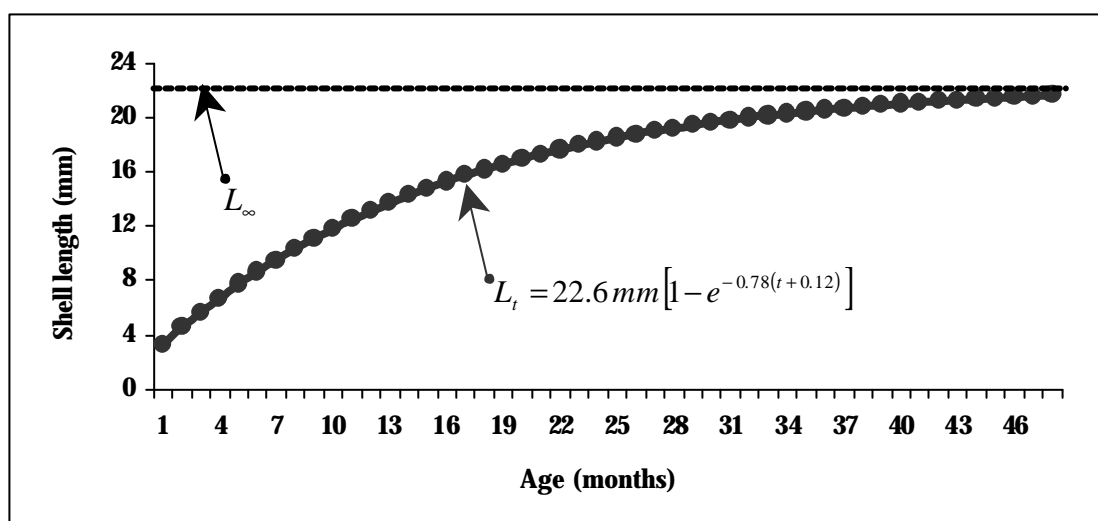


Figure 4.3. Von Bertalanffy growth (VBG) curve of *N. pullus* from Arakan. L_{∞} : asymptotic length (theoretical maximum shell length = 22.6 mm), K : growth coefficient parameterizing the rate of growth (= 0.78 year⁻¹).

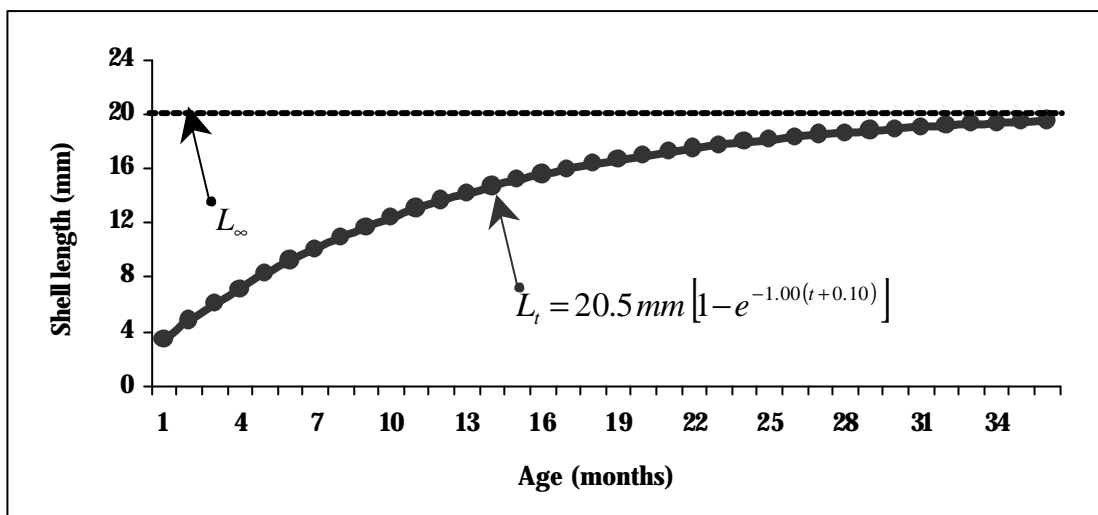


Figure 4.4. Von Bertalanffy growth (VBG) curve of *N. bimaculosus* from Likupang. L_{∞} : asymptotic length (theoretical maximum shell length = 20.5 mm), K : growth coefficient parameterizing the rate of growth (= 1.00 year⁻¹).

4.3.2 Recruitment patterns

The FISAT analysis of temporal recruitment patterns indicates that recruitment takes place throughout the whole year in both *N. pullus* and *N. bimaculosus* (Figure 4.5). It was not possible to decompose the monthly pattern into distinct normal components, suggesting that there are no pronounced seasonal recruitment pulses. However, it was evident in both species that recruitment was higher in the wet and wet-dry intermediate seasons than in the dry season.

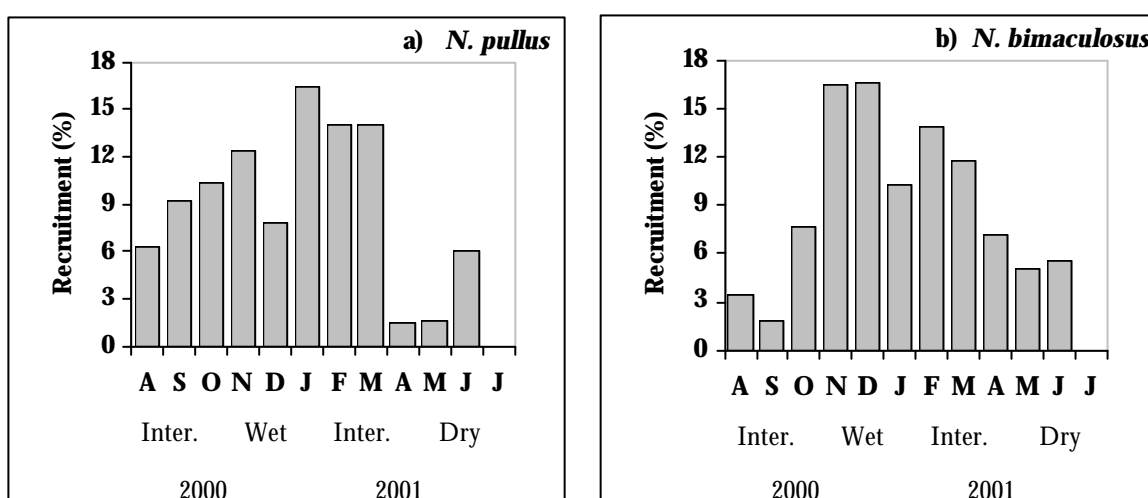


Figure 4.5. Monthly recruitment patterns of (a) *N. pullus* from Arakan and (b) *N. bimaculosus* from Likupang between August 2000 and July 2001.

I checked whether the relative recruitment proportion in each months was related to key environmental factors (temperature and salinity), which can be assumed to affect recruitment. In case of *N. pullus*, the highest relative recruitment coincided with decreased temperatures and decreased salinities during the wet season while the lowest recruitment during the dry season was accompanied by high temperatures (Figure 4.6). Hence, there was a significant correlation between relative recruitment and temperature (Spearman's rank correlation $\rho_s = -0.731$, $p = 0.011$) but not between recruitment and salinity ($\rho_s = -0.266$, $p = 0.430$).

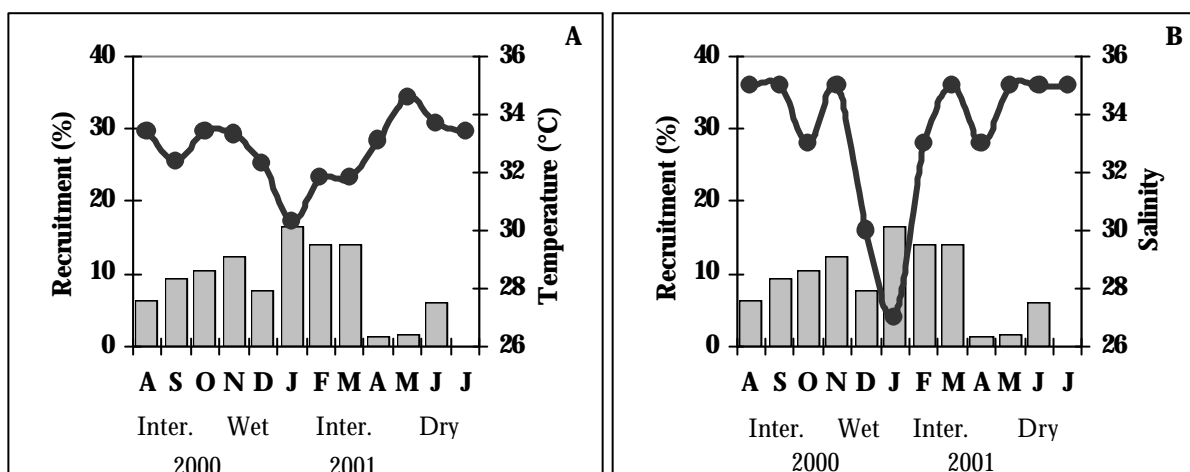


Figure 4.6. *N. pullus* from Arakan. Monthly recruitment pattern (■) between August 2000 and July 2001 in relation to (a) temperature (●) and (b) salinity (●).

For *N. bimaculosus*, a similar trend in the relation between recruitment, temperature and salinity was discernible (Figure 4.7). However, these relations were not as pronounced, as the rather low (and statistically not significant) correlation coefficients indicate (recruitment–temperature $\rho_s = -0.041$, $p = 0.905$; recruitment–salinity $\rho_s = -0.542$, $p = 0.085$).

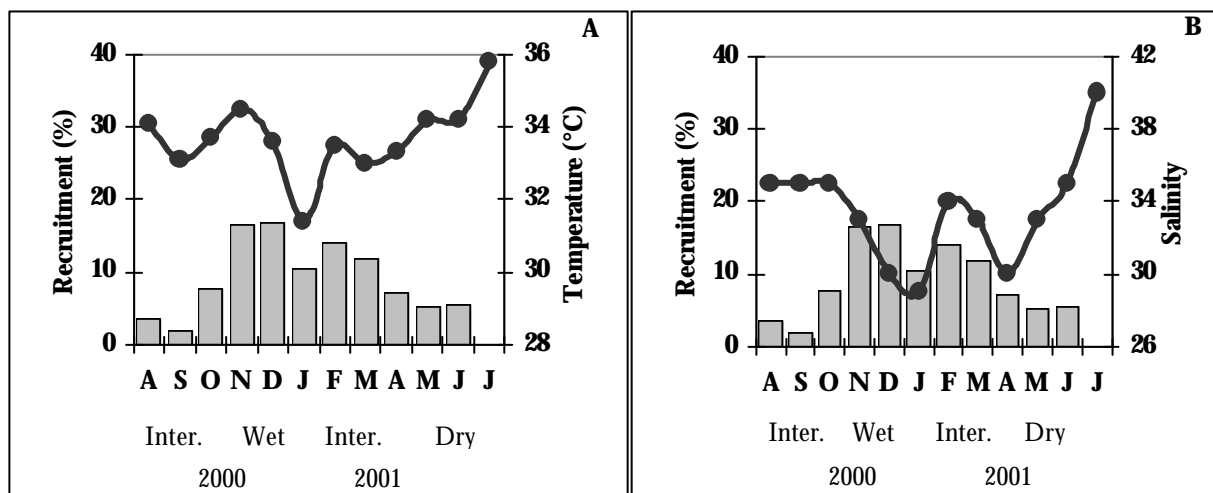


Figure 4.7. *N. bimaculosus* from Likupang. Monthly recruitment pattern (■) between August 2000 and July 2001 in relation to (a) temperature (●) and (b) salinity (●).

4.3.3 Mortality

Using the 'length-converted catch curve' (LCCC) approach, the sizes of the investigated nassariid specimens were converted into relative ages. *N. pullus* reached in size from 6 mm-below to 21 mm-below, corresponding to relative ages from 0.43 to 3.84 years (Table 4.3). The individuals of *N. bimaculosus* fell into a size range from 6 to 19 mm-below, equalling a range of relative ages from 0.38 to 3.00 years (Table 4.4).

Table 4.3. *N. pullus* from Arakan. Conversion of length classes (mm-below) into relative ages (years) using the 'length-converted catch curve' (LCCC) approach. dt: relative age range (year) of each size class; $\ln(N/dt)$: log-transformed number of individuals N in each length-converted age class. Bold values were used to estimate the mortality rate Z .

<i>Size Class</i>	<i>N</i>	<i>Rel. age</i>	<i>dt</i>	$\ln(N/dt)$
6	1	0.4313	0.0715	2.6373
7	2	0.5133	0.0762	3.2664
8	2	0.6010	0.0817	3.1980
9	12	0.6951	0.0879	4.9163
10	16	0.7966	0.0952	5.1247
11	16	0.9069	0.1037	5.0386
12	23	1.0276	0.1140	5.3072
13	27	1.1609	0.1265	5.3635
14	29	1.3096	0.1421	5.3187
15	41	1.4779	0.1621	5.5335
16	72	1.6716	0.1886	5.9450
17	124	1.8999	0.2255	6.3097
18	178	2.1779	0.2805	6.4530
19	94	2.5334	0.3712	5.5343
20	12	3.0268	0.5499	3.0828
21	6	3.8395	1.0809	1.7140

Table 4.4. *N. bimaculosus* from Likupang. Conversion of length classes (mm-below) into relative ages (years) using the 'length-converted catch curve' (LCCC) approach. dt: relative age range (year) of each size class; $\ln(N/dt)$: log-transformed number of individuals N in each length-converted age class. Bold values were used to estimate the mortality rate Z .

<i>Size Class</i>	<i>N</i>	<i>Rel. age</i>	<i>dt</i>	$\ln(N/dt)$
6	5	0.3783	0.0642	4.3556
7	16	0.4522	0.0691	5.4448
8	22	0.5320	0.0749	5.6833
9	35	0.6188	0.0816	6.0608
10	46	0.7139	0.0898	6.2389
11	57	1.8189	0.0998	6.3481
12	49	0.9363	0.1122	6.0793
13	80	1.0693	0.1282	6.4362
14	156	1.2227	0.1495	6.9501
15	192	1.4040	0.1794	6.9756
16	196	1.6257	0.2243	6.7731
17	95	1.9109	0.2992	5.7604
18	11	2.3114	0.4508	3.1946
19	2	2.9899	0.9368	0.7585

The mortality Z was estimated from the descending right arms of the length-converted catch curves (Figure 4.8). For *N. pullus*, only specimens of a size of at least 17 mm-below and a (relative) age of 1.9 years were considered. For *N. bimaculosus*, the lower boundary was 14 mm-below and 1.2 years, respectively.

The linear regressions fitted to the descending right arms of the LCCCs were highly significant for both species (Table 4.5 and Table 4.6), the correlation coefficient was -0.97 in both cases. The slope of the regression line, i.e., the mortality rate Z , of *N. pullus* was $2.64 \pm 0.38 \text{ year}^{-1}$ ($\pm 95\%$ confidence interval CI), corresponding to a yearly mortality proportion of $93\% \text{ year}^{-1}$ (CI: 90 to $95\% \text{ year}^{-1}$). For *N. bimaculosus*, the Z value was $3.77 \pm 0.42 \text{ year}^{-1}$, which is equivalent of a yearly mortality proportion of $98\% \text{ year}^{-1}$ (CI: 96 to $98\% \text{ year}^{-1}$). Since the 95%

confidence intervals of the two Z values do not overlap, the mortality rate of *N. bimaculosus* is significantly higher than that of *N. pullus*.

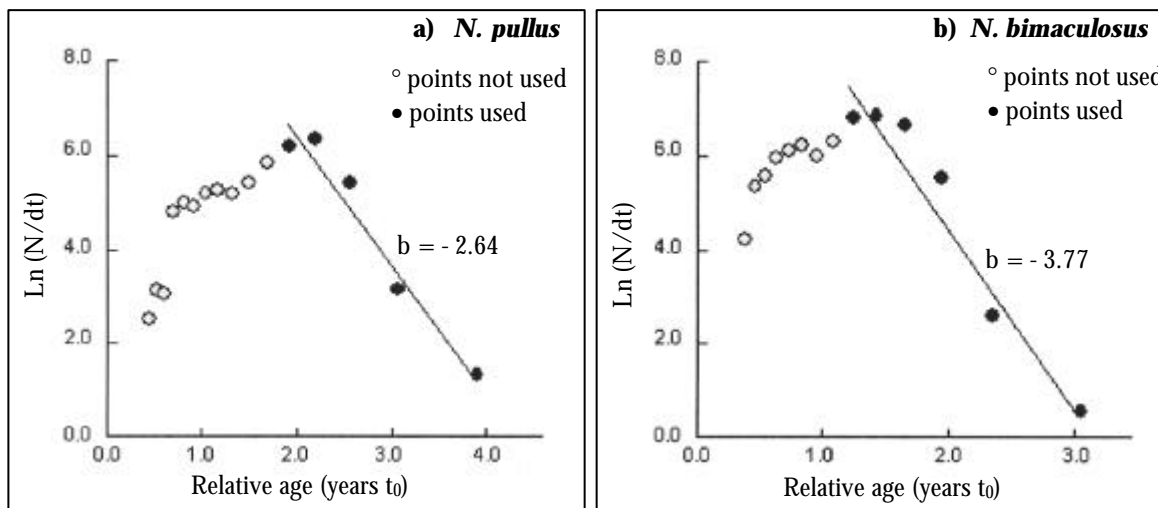


Figure 4.8. Length-converted catch curve for (a) *N. pullus* from Arakan and (b) *N. bimaculosus* from Likupang Full points were included in the computation of the regression used to estimate the mortality rate Z.

Table 4.5. *N. pullus*. Results of the ANOVA of the regression performed with the selected data points of the length-converted catch curve (LCCC). df: degrees of freedom; SS: sum of squares; MS: mean square; F: F statistic; R: correlation coefficient; CI: confidence interval.

Sources	df	SS	MS	F
Regression	1	17.15	17.15	48.03
Residual	3	1.07	0.36	
Total	4	18.22		
Multiple R	-0.97		95 % CL	
Intercept (a)	11.68		1.07	
Variable (b)	-2.64		0.38	

Table 4.6. *N. bimaculosus*. Results of the ANOVA of the regression performed with the selected data points of the length-converted catch curve (LCCC). df: degrees of freedom; SS: sum of squares; MS: mean square; F: F statistic; R: correlation coefficient; CI: confidence interval.

Sources	df	SS	MS	F
Regression	1	31.75	31.75	81.89
Residual	4	1.55	0.39	
Total	5	32.29		
Multiple R	-0.97		95 % CL	
Intercept (a)	12.21		1.07	0.84
Variable (b)	-3.77		0.38	0.42

4.3.4 Longevity

The largest specimens of *N. pullus* and *N. bimaculosus* that I found during my study had shell lengths (L_c) of 21.5 mm and 19.4 mm, respectively. These values are approximately 5% smaller than the asymptotic lengths L_∞ of the von Bertalanffy growth models (22.6 mm and 20.5 mm, respectively). If $L_c = 0.95 L_\infty$, the longevity of can be estimated by dividing 3 by the VBG growth coefficient K (Taylor, 1965). Using this approach, the longevity of *N. pullus* is estimated to be 3.85 years (46 months) and that of *N. bimaculosus* 3.00 years (36 months).

4.4 Discussion

4.4.1 Growth

Growth is among the key attributes of live organisms. It is actually an individual feature, i.e. each specimen of a population has its own unique growth pattern during its life, depending on both genetic heredity and environmental factors. However, as growth is usually quite similar among all specimens of a certain population at a certain site, it can be described by growth function parameters modelling the growth of an "average individual". Therefore, growth is also a fundamental parameter in population dynamics. Without information on it, population parameters such as mortality, longevity or productivity cannot be determined.

Basically, there are three approaches to measure growth and to determine the growth parameters: (1) analysis of size-at-age data, (2) study of size-increment data, and (3) analysis of size-frequency data. The first method requires the assessment of the absolute age of individuals, e.g. by counting annual growth marks that many benthic animals exhibit in their shells or certain skeletal elements. For example, Tallmark (1980) applied this approach in his study on *N. reticulatus* from Gullmar Fjord, Sweden. However, in case of tropical species the determination of the absolute age of an individual is much more difficult, as pronounced annual growth marks are usually absent because seasonal differences in growth, if any, are hardly pronounced. The size-increment approach does not require any information on individual age but is based on the repeated measurement of the sizes of the same individuals at given time intervals. Growth is directly determined as size difference between two (or more) measurements. In the field, this method requires the retrieval of measured specimens through either the growth-mark or the tagging-recapture technique. This approach has been applied for temperate nassariids by, e.g., Tallmark (1980). It is quite elaborate and does not work well in case of rather low abundance and high mortality of the organisms under study. Therefore, I used the third approach, the analysis of size-frequency data, to determine the growth of *N. pullus* and *N. bimaculosus* off northern Minahasa.

The growth parameters K of the von Bertalanffy growth (VBG) model fitted to the size-frequency data of *N. pullus* and *N. bimaculosus* indicate that both species grow quite fast ($K = 0.78$ and $K = 1.00$, respectively). The basic characteristic of the VBG model is that growth is particularly fast in young and small specimens and gradually levels off with increasing age and size. In both species, the smallest individuals in my samples were juveniles with shell lengths of 6 mm-below. According to the VBG model, these specimens presumably settled 4 (*N. pullus*) and 3 (*N. bimaculosus*) months ago and grew at a rate of 1.1 and 1.3 mm per month. *N. pullus* needed further 14 months, growing at continuously decreasing monthly growth rates of 1.0 to 0.4 mm/month, to reach sexual maturity at an average age of 1.5 years and an average size of 16 mm. *N. bimaculosus* grew a bit faster, at rates of 1.2 to 0.5 mm/month, before it attained sexual maturity at an average age of about 1 year and an average size of 14 mm-below. The growth of

mature individuals continued to decrease markedly in both species and was less than 0.1 mm/month at the end of the natural life span (3.85 and 3.00 years, respectively) when they could have reached lengths of up to 21.5 and 19.4 mm, respectively. Such an ontogenetic growth pattern (growth decreases with age) can be found in virtually all multicellular animals and has also been reported for other nassariids, such as *N. obsoletus* (Scheltema, 1964) and *N. reticulatus* (Tallmark, 1980). It is related to a fundamental size-dependent decrease in metabolic rates and reflects a strategy to shift the energy allocation from somatic production (= growth) to reproduction.

Besides the universal ontogenetic pattern in growth, there is a general trend with regard to latitude as well. It is well documented that molluscan growth – as well as metabolic rates in general – increases with temperature and, hence, is commonly higher in the tropics than at higher latitudes (Frank, 1969; Ansell et al, 1972; Beukema & Meehan, 1985).

Only few comparative data are available on the growth of tropical nassariids. Thivakaran (1984) reported that *N. stolata* from Porto Novo, India, attained lengths of 8.2, 11.7, 13.8, 15.4 and 16.4 mm after its first, second, third, fourth and fifth year of life, respectively, which translate to average monthly growth rates of 0.7 mm, 0.3 mm, 0.2 mm, 0.1 mm and 0.1 mm, respectively. These values are markedly smaller than the ones I estimated for *N. pullus* and *N. bimaculosus* but this might primarily reflect methodological rather than biological differences. There are more reports on the growth performance of temperate and sub-tropical *Nassarius* species. Scheltema (1964) found that *N. obsoletus* from Massachusetts grew at a rate of 1.3 to 1.4 mm a month and attained sexual maturity at a shell length of 12 to 14 mm three years after settlement (Scheltema, 1964). In Sweden, the same species became sexually mature at a length of 15 mm during the fourth year after settlement (Tallmark, 1980). McKillup (1979) reported that *N. pauperatus* from central Queensland, Australia (35° S), becomes sexually mature at a size of 19 mm within 15 months after settlement, while *N. dorsatus* from Queensland, Australia (23° S) grew more rapidly than expected (0.8 mm a day), attaining a length of 10 mm in only 10 days (McKillup & McKillup, 1997). These values are comparatively high when compared to my results. However, most of these data were determined for young and, hence, fast growing individuals. Therefore, they are not directly comparable to mine. In general, inter-site comparisons of growth rates determined by different authors are always ambiguous because they can easily be confounded through differences in assessment methods used.

4.4.2 Recruitment patterns and population structure

The most striking finding in the analysis of the dynamics of the monthly size distributions of *N. pullus* and *N. bimaculosus* was that throughout the whole study year the size group containing the largest and oldest specimens clearly formed the majority of the intertidal

populations. This general pattern was evident in both species, for *N. pullus* even more pronounced than for *N. bimaculosus*. The FISAT analysis suggested that juvenile specimens recruited to the populations in the study area throughout the entire year. But although in both species the recruitment appeared to be somewhat stronger during the wet than during the dry season, there was no evidence of clear recruitment pulses. The most striking result, however, was that the recruits were never very numerous and did not account for a considerable part of the population at any time. Hence, it was difficult to identify distinct cohorts (as discrete modes in the size-frequency distributions) that could be tracked through the series of monthly histograms.

The basic result that large and old individuals outnumbered the small and young ones at any given time is a surprising finding. There are several possible explanations for this pattern:

- 1) Specimens smaller than 16 mm-below in *N. pullus* and 14 mm-below in *N. bimaculosus* were collected with markedly lower efficiencies than larger specimens (and, hence, the monthly histograms were not representative, i.e. they did not reflect the true size-frequency distribution).
- 2) Recruitment was – for unknown reasons – exceptionally low throughout the entire one-year study period.
- 3) The intertidal study area did not contain the entire population, i.e. the smaller specimens preferably inhabit habitats outside of the intertidal area covered by my survey.

I rule out the first possibility. Because of the sampling procedure applied here (see chapter 4.2.1), I regard it as very unlikely that the abundances of the specimens of 5 to 16 mm length are underestimated to such a degree that the methodological bias alone would explain the extremely left-skewed size-frequency distributions. Hence, the general finding that young specimens are markedly rarer than old ones in the intertidal study areas off Arakan and Likupang is very probably valid. Furthermore, I regard the third explanation as more probable than the second one. It is very likely that the majority of the juvenile individuals of the populations under study do not occur in the investigated intertidal areas but instead live in – probably adjacent – habitats that I have not surveyed during my study. From there, they do not immigrate to the intertidal flats before they have attained sexual

Although marked recruitment pulses were not discernible in my data, there was some evidence that the recruitment was lower during the comparatively warm dry season than during the wet season when temperatures were about 3 to 4 °C lower. However, it should be noted that even then the values were still above 30 °C. Yet, a correlation analysis indicated that, at least for *N. pullus* from Arakan, reduced recruitment was related to increased temperatures. This hypothesis seems plausible, considering that during midday low tides temperatures in tide pools on the sand flats can easily exceed 40 °C and many tide pools run dry. Even under these

extreme conditions, most adult nassariids still thrive, as they keep on creeping over the sand flat and do not bury themselves to avoid temperature and desiccation stress. Young recruits, however, might be more affected. In case of *N. pauperatus* from southern Australia, settling recruits have been observed to die at temperatures of 38 to 44 °C (McKillup et al., 1995). In contrast to temperature, there was no significant correlation between recruitment and salinity in my data, although this factor also varies between wet and dry seasons. Scheltema (1965) reported that young *N. obsoletus* showed normal growth at a salinity of 32.9 but died at values < 16. Cheung (1977) found that *N. festivus* from western Hong Kong exhibit a decrease in feeding activity and reproductive output (mean number of eggs per capsule) at salinity value of 15 ‰. However, such low salinities were not recorded during my study.

Recruitment success of intertidal species is determined by a variety of processes acting during various life cycle phases: gonad development and spawning of adults, larval stage (which may be planktonic), and settlement and establishment of post-larvae on the seabed (Bowman & Lewis, 1977). Therefore, the recruitment at a given site is hard to predict, since the recruits can actually come from somewhere else and their supply is mostly determined by factors operating outside the study area (Underwood, 1975). Among prosobranch gastropods closely related to the genus *Nassarius*, some species have free-swimming planktotrophic larvae, while others propagate by direct development (Tallmark, 1980) or free-swimming but non-planktotrophic larvae (Jablonski & Lutz, 1983). The reproduction mode of *N. pullus* and *N. bimaculosus* is not known. They might have planktotrophic larvae, like other species such as *N. pauperatus* (McKillup & McKillup, 1997), or non-planktotrophic larvae, like *N. reticulatus* or *N. incrassatus* (Lebour, 1931). This would mean in both cases that recruitment does not directly depend on the reproduction of the adult stock inhabiting the study areas but also on the number of larvae that originate from other areas and are transported with tidal currents on the intertidal sand flats investigated off Arakan and Likupang. Thus, recruitment would be heavily affected by the supply of such allochthonous larvae (which is mostly regulated by some large-scale pelagic processes) and the survival of settled post-larvae at the study sites (which is determined by local factors, such as the suitability of settling substrates, the presence of sufficient food, or predation pressure, incl. possible cannibalism). I cannot tell which factors regulated both the supply and survival of nassariid recruits – and, hence, I cannot explain the spatial and temporal variation in recruitment – as I did not take pelagic samples to look at the amount of imported meroplanktonic larvae and I did not observe the actual process of post-larval settlement during my study. However, McKillup et al. (1993) proposed that wide and gently-sloping sand flats, like those off Arakan and Likupang, are ideal settling grounds for nassariid recruits. McKillup et al. (1993) also speculated about the role of cannibalism on the survival of recruits, as adults may feed on their own eggs when carrions as their prime food source are in short supply. I did not observe any direct evidence for this in the field (on the contrary, there are plenty of cadavers available on the investigated sand flats; see below). Furthermore, my data are not sufficient to

discern a negative relationship between adult stock and recruitment, which would suggest an effect of cannibalistic behaviour.

4.4.3 Mortality and longevity

Mortality is a key process regulating size and structure of a population. It is caused by various processes, such as episodic events of simultaneous mass mortality induced by habitat disturbances, e.g. an oil spill, genetic limits of longevity determining the life span of a species, and the monotonous decrease in number of an age class with time, a process caused by resource competition or predation, parasitism and diseases. The latter is the most important type of mortality (Brey, 2003). Although the mortality may vary with age (it is usually markedly higher for larvae and senile specimens than for mature adults), the overall death pattern averaged across the entire life of a cohort can be adequately modelled by a single negative exponential mortality equation, which features Z , the instantaneous rate of mortality, as sole parameter describing the slope of the decrease of individuals over time (Brey, 2003). Z summarizes the effects of all – natural and, possibly, anthropogenic – mortality causes acting throughout the life of a cohort.

There are several approaches to estimate Z in natural populations. One of the most often methods, particularly if the age of individuals is difficult to assess, is the 'length-converted catch curve' (LCCC), which combines the information drawn from size-frequency distributions and the von-Bertalanffy growth model (Sparre & Venema, 1998). A LCCC usually has an ascending left arm and a descending left arm. The former represents specimens that are too small and young to be fully recruited and/or fully disposed to the sampling method used. The points of the left arm are thus severely downward biased and, hence, are not considered when the mortality is estimated by the slope of a regression line fitted to the points of the descending right arm. Using the LCCC approach, the mortality Z of *N. pullus* was estimated to be 2.64, which was significantly smaller than that of *N. bimaculosus* ($Z = 3.77$). Both are quite high mortality rates, meaning that 93% of the individuals of a cohort of *N. pullus* and 98% of a *N. bimaculosus* cohort die within one year. However, both estimates are probably too high. In the right LCCC arms only mature large and old specimens were represented (= 17 mm-below and = 1.9 years for *N. pullus*, = 14 mm and 1.2 years for *N. bimaculosus*), because for unknown reasons (see above) smaller and younger individuals were markedly less abundant in the samples and, consequently, could not be considered in the LCCC method. Therefore, the above-mentioned Z estimates measure primarily the mortality of rather old adult animals, which is probably higher than the overall cohort mortality. However, in conclusion I assume that the Z values are indeed upward biased to a certain degree but the basic finding of quite high mortality in the two investigated *Nassarius* species is still valid because it fits into a fundamental pattern relating growth, mortality and longevity (Ebert, 1973): as for most tropical invertebrate benthos

species, high mortality is coupled with rapid growth (see above) as well as low longevity (see below).

The biological factors possibly causing mortality of nassariid snails (resource competition, predation, parasitism, diseases) were not directly investigated. During the survey, I found numerous empty *Nassarius* shells, but time and cause of the deaths of their former bearers remain unknown. Some shells featured a hole in the back of the body whorl but it was not possible to answer the questions which predator caused this hole and whether the attack had been fatal. I occasionally observed that some snails were killed by hermit crabs, but the effect of crab predation on the snail populations cannot be quantified. The snails' behaviour of burying themselves in the sediment may be a defence mechanism against predation by crabs, as it has been proposed for *N. obsoletus*, *N. vibex* and *N. trivittatus* from Massachusetts (Stenzler & Atema, 1977). Most shells were largely intact, and in these cases the mortality causes cannot be deduced.

Resource competition may also be an important factor contributing to mortality, especially if the resource is non-renewable, i.e. if it is monopolized by the exploiting organism and is not available after use anymore (Levinton, 1995). Nassariids are primarily scavengers, and their prime food, carrions, is certainly a non-renewable resource. Furthermore, the occurrence of carrion is spatially and temporally not predictable (Britton & Morton, 1994) and may thus be a limiting factor of nassariid densities (McKillup & McKillup, 1997). However, in case of the flats off Arakan and Likupang shortage of carrion is very unlikely to cause mortality among the populations of *N. pullus* and *N. bimaculosus*, because of the ample supply of carcasses provided by the discarded by-catch of local fisheries (own observation). This is a good example of an indirect effect of human interference on mortality patterns. The direct anthropogenic effect of exploiting the nassariid populations as a fishery resource, causing the so-called fishing mortality, is very probably negligible at present, because the snails are too small to be used for human consumption. However, this might change in the future, in case the nassariids will be increasingly used as fishing baits or as sources for handicrafts.

The longevity of *N. pullus* and *N. bimaculosus*, i.e., the age that only 1 out of 100 individuals of a population will reach, was estimated from the growth parameter K of the von Bertalanffy growth (VBG) model ($= 3/K$; Taylor, 1965) to be 3.85 years and 3.00 years, respectively. The largest specimens found in my survey ($L_{\max} = 21.3$ mm for *N. pullus*, $L_{\max} = 19.5$ mm for *N. bimaculosus*) were probably of these ages. These values agree quite well with the ones reported for other tropical nassariids (Table 4.7).

Apparently, 5 years seems to be an upper limit of longevity, and most species do not grow much larger than 20 mm, except of the Indian species *Bullia vittata* that can reach an exceptionally large maximum size of 50 mm (Thilaga et al., 1987). There are exceptions, but in general temperate species get markedly older (> 15 years) and grow distinctly larger (up to 30 years) than tropical ones (Table 4.7).

Table 4.7. Longevities and maximum lengths (L_{\max}) of nassariid species from tropical and temperate study sites. na: not available

Species	Location	L_{\max} (mm)	Longevity (years)	Source
Tropical:				
<i>Nassarius bimaculosus</i>	Northern Minahasa, Indonesia	19.5	3.9	Present study
<i>N. pullus</i>	Northern Minahasa, Indonesia	21.3	3	Present study
<i>Nassa stolata</i>	Porto Novo, India	16.4	4	Thivakaran, 1984 (cited in Thilaga et al, 1987)
<i>Bullia vittata</i>	Porto Novo, India	50.2	4 – 5	Thilaga et al, 1987
Temperate:				
<i>N. obsoletus</i>	Massachusetts, USA	na	< 5	Scheltema, 1964
<i>N. reticulatus</i>	Gullmar Fjord, Sweden	30	15	Tallmark, 1980
<i>N. reticulatus</i>	south-western England	30	18	Bryan et al, 1993
<i>Bullia rhodostoma</i>	Algoa Bay, South Africa	na	20	McLachlan et al, 1979

There is obviously a compensation between growth and longevity along a gradient in latitude and temperature (Frank, 1969): growth is faster in warm tropical than in cooler temperate regions, while for longevity and maximum size the opposite trend is evident.

Chapter 5

REPRODUCTION

5.1 Introduction

The two species *N. pullus* and *N. bimaculosus*, which form the subject of this chapter, are widely distributed off the coasts of the Northern Minahasa Peninsula, Indonesia. Their high population densities together with their distribution suggest that these species have important roles in the energetics of the intertidal ecosystem they inhabit.

Like other neogastropods, *Nassarius* species are usually dioecious and reproduce by internal fertilization (Fretter, 1941). Since Smith (1971, 1980) gave the first report on penis bearing females for the North American species *N. obsoletus*, other authors have also provided the same information for *N. vibex* (Demaintenon, 2001 a, 2001 b) and other European species, including *N. reticulatus* (Stroben et al., 1992; Barroso & Moreira, 1998; Barreiro et al., 2001). These species showed evidence of an abnormal reproductive organ structure, called imposex (Smith, 1971) or pseudohermaphroditism (Jenner, 1979). Reproductive systems of males, females and females with imposex show various degrees of expression related to the annual reproductive cycle, the age of the animals and stress factors. Houston (1971) reported on the spawning and egg capsules of the American species *N. tiarula* while Grachtrup (1991) thoroughly studied the early development of the European species *N. reticulatus* under the microscope. Tallmark (1980) and Lambeck (1984) studied migrations, growth and age, biomass, recruitment and mortality of *N. reticulatus*. Barroso & Moreira (1998) did a similar study; however, they focused on the gametogenesis process in the reproduction cycle of *N. reticulatus*.

In light of the various studies on temperate *Nassarius* populations, it was of interest to investigate the reproductive biology of Indonesian *Nassarius* species, because this has not been done before. Biological studies on reproduction are of great value in ecological investigations since they provide important data related to the population structure and allow accurate predictions concerning recruitment patterns (Seed & Brown, 1977).

5.2 Materials and methods

The field work was carried out at Arakan and Likupang. *N. pullus* (10 – 19 mm-below in shell length) and *N. bimaculosus* (10 – 18 mm-below in shell length) were collected by hand from shallow water during spring low tides between August and October 2002. Only snails with a shell length greater than 10 mm were selected, assuming that they were beginning to develop sexually. All individuals were preserved in Bouin's solution for 24 hours and then preserved in 70% ethanol for histological study.

In the laboratory, a total of 160 specimens each of *N. pullus* from Arakan and Likupang, respectively, and a total of 150 specimens of *N. bimaculosus* from Likupang were examined. Shell length was measured with dial callipers. The shell was then carefully broken using a hammer. Using a small forceps, the individuals were removed from the shells. The bodies were dehydrated in gradually increasing concentrations of ethanol and then placed in toluene for clearance overnight. They were then embedded in paraffin wax (4 individuals in each block). The samples were sectioned in 7 μ m slices with a microtome to make them clearly visible under a light microscope. Haematoxylin and eosin staining procedures were applied according to Mc Manus & Mowry (1965).

The histological preparations were examined under a dissecting microscope (Leica IM 1000) at magnifications of 10x to 40x. Gonad development stages were categorized based on the criteria of Seed & Brown (1977) and Jasim & Brand (1989) as modified by Baroso & Moreira (1998). Developmental stages of female gonads (Figure 5.1) were classified into:

- *Proliferation stage (I)*: first young oocytes appear, but they do not fill the gonad cavity; oocyte cytoplasm looks smooth in the haematoxylin-eosin stained preparation
- *Early development stage (II)*: oocytes have grown in size and numbers but still do not completely fill the gonad cavity
- *Late development stage (III)*: gonad is full of oocytes most of which are ripe (featuring a granular cytoplasm in the stained sections) but still there are also some developing oocytes
- *Spawning stage (IV)*: gonad is full of ripe, polygonal or spherical, densely-packed oocytes
- *Post-spawning stage (V)*: gonad is much smaller, it contains only a few unspawned oocytes which will be resorbed

For males, an analogous scheme for rating the stage of the testes was used. However, using light microscopy I could only differentiate between stage III and IV (Figure 5.1). For stage V of female gonads, I used the term 'post-spawning' instead of 'spent' or 'resting' because this stage is only very short or even absent in tropical species. It is very similar to the early stages of each reproduction cycle, in which ovaries cannot be distinguished from testes unless a transmission electron microscope is used.

Individuals that could not be sexed because there was no gonad detectable are regarded as juveniles. Stages III and IV are considered as reproductively active stages, while juveniles and stages I, II and V are reproductively inactive stages.

Individuals were designated as 'sexually mature' if the gonads were indicative of stage III or higher. The shell length at which 50% of all individuals were sexually mature (L_{50}) was estimated from the proportion of mature individuals in each 1-mm length class between 10 and 19 mm-below.

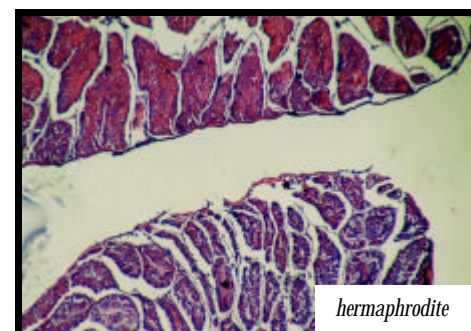
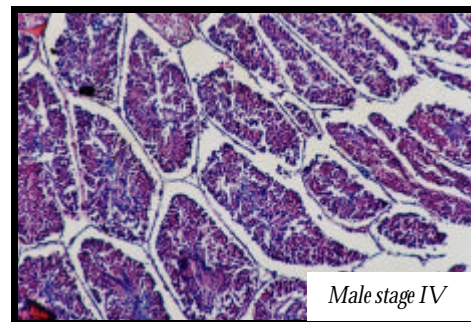
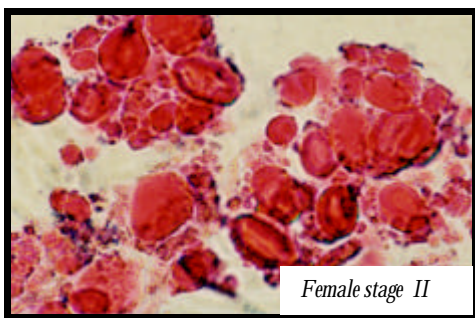
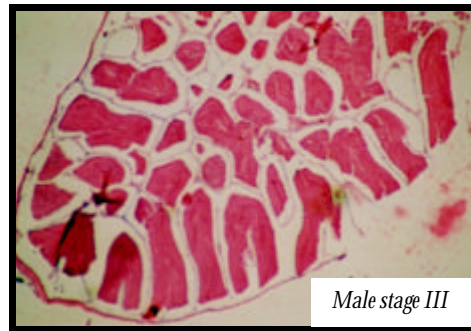
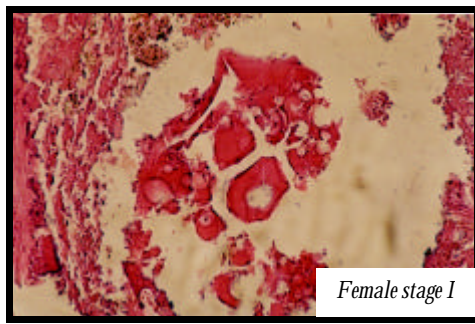


Figure 5.1. *N. pullus*. Some stages of gametogenesis of the testes and ovaries (indicated on the bottom right hand side)

Sex ratios are expressed as the proportion of females, i.e as the ratio of the number of females to the total numbers of females and males.

Some individuals of *N. pullus* had gonads which contained both oocytes and spermatocytes. The term 'abnormal' is used for such individuals and gonads because it was not clear whether this condition was a normal phase in the ontogeny of the species (then called 'hermaphroditism') or was caused by external stress factors (in this case called 'imposex' or 'pseudohermaphroditism').

5.3. Results

5.3.1 Size at maturity

All histological sections of *N. pullus* from Arakan and Likupang and of *N. bimaculosus* from Likupang were examined to determine the gonad development stage. Figure 5.2 shows the proportion of mature specimens, i.e. those with gonads in stage III, IV or V, in each length class between 10 and 19 mm-below.

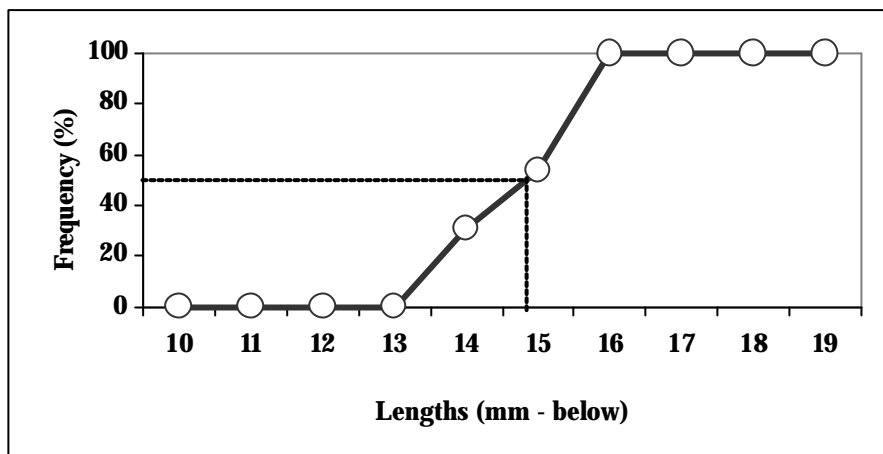
At both Arakan and Likupang, the smallest mature *N. pullus* had a shell length of 14 mm-below (Figures 5.2a and 5.2b). Sizes at maturity (L_{50}) were 15 mm-below in both cases. At Likupang, some specimens > 18 mm-below could not be sexed and staged as the gonads were not distinguishable in the microscopic sections.

There is evidence that *N. bimaculosus* from Likupang matured at a smaller size than *N. pullus* (Figure 5.2c). The smallest mature specimens had shell lengths of 13 mm-below, and L_{50} was estimated to fall into the same size class. As for *N. pullus* from Likupang as well, there were some larger specimens (17 mm-below) which did not feature a microscopically discernible gonad and, hence, could not be sexed and classified in terms of their development stage.

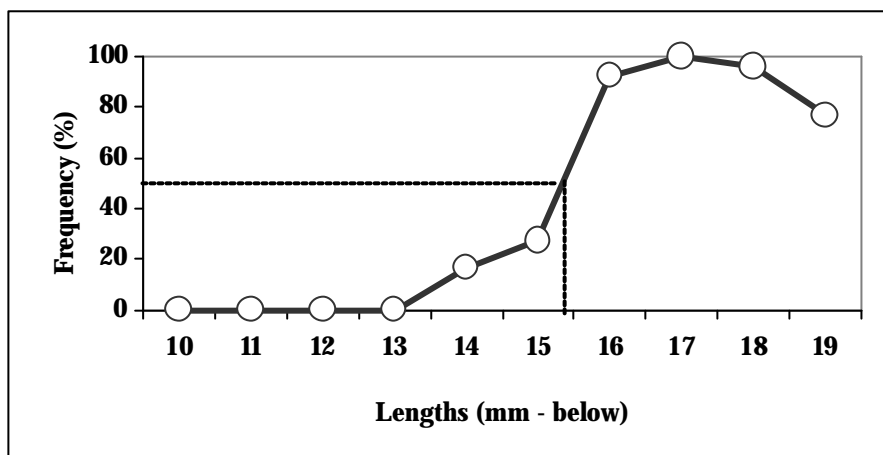
5.3.2 Sex ratio

At Arakan, a total of 106 mature individuals of *N. pullus*, ranging in shell length from 14 to 19 mm-below, were found (Table 5.1). Of these, 54 were female, 38 were male and 14 had 'abnormal' gonads, i.e. the sex ratio was not significantly different from 0.5 ($\chi^2 = 2.78$, $p = 0.095$; 'abnormal' individuals not included). In each single month between August and October, there were more females than males. However, these differences were not significant (χ^2 tests, $p > 0.05$). Females also dominated each length class between 14 and 18 mm-below but according to χ^2 tests they were only at one size (17 mm-below) significantly more frequent (Table 5.2; $\chi^2 = 4.17$, $p = 0.041$).

a) *N. pullus*, Arakan



b) *N. pullus*, Likupang



c) *N. bimaculosus*, Likupang

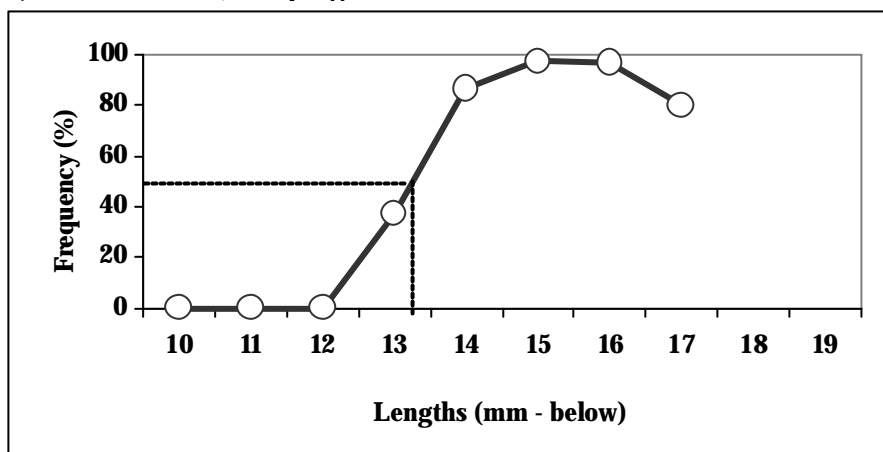


Figure 5.2. Frequencies (%) of mature specimens vs shell length in *N. pullus* from a) Arakan (n=160) and b) Likupang (n=160); c) *N. bimaculosus* (n = 150) from Likupang

Table 5.1. Monthly distribution of sexes in *N. pullus* from the Arakan

Months	Unsexed	Males	Females	Sex Ratio	c ²	p value	'Abnormal'
August	14	26	33	0.56	0.83	0.362	9
September	18	5	10	0.67	0.89	0.346	3
October	22	7	11	0.61	1.67	0.197	2
Totals	54	38	54	0.59	2.78	0.095	14

Across the size range, the proportions of the sexes did not change significantly ($\chi^2 = 9.02$, $p = 0.108$). Abnormal hermaphroditic individuals did occur only at sizes = 16 mm-below, and there was no trend of an increase or decrease with size.

Table 5.2. Size distribution of sexes in *N. pullus* from the Arakan

Shell (mm)	Males	Females	Sex Ratio	c ²	p value	'abnormal'
14	1	3	0.75	1.00	0.317	0
15	2	5	0.71	1.29	0.257	0
16	4	7	0.64	0.82	0.366	2
17	7	17	0.71	4.17	0.041*	6
18	7	13	0.65	1.80	0.180	3
19	17	9	0.35	2.46	0.117	9

At Likupang, I recorded a total of 94 mature *N. pullus* (Table 5.3). Across the three months from August to October, females were significantly more frequent than males (57 vs. 22; $\chi^2 =$

15.51, $p < 0.0001$; a total of 22 'abnormal' individuals not included. Within months, there were always >100% more females than males but because of the rather small sample sizes χ^2 tests could confirm the statistical significance of these differences only for August ($\chi^2 = 9.80$, $p < 0.002$). Females were also in the majority across the entire size range between 14 and 19 mm-below (Table 5.4). At 14 and 15 mm-below, there were no males at all, and at 17 and 18 mm-below the numerical superiority of females was statistically significant (χ^2 tests, $p < 0.05$).

Table 5.3. Monthly distribution of sexes in *N. pullus* from Likupang

Months	Unsexed	Males	Females	Sex Ratio	c ²	p value	'Abnormal'
August	22	12	33	0.73	3.80	0.002**	6
September	23	5	12	0.71	2.88	0.009	5
October	21	5	12	0.71	2.88	0.009	4
Totals	66	22	57	0.72	15.81	< 0.0001***	15

There were no significant changes in the proportions of males and females among the size classes ($\chi^2 = 5.79$, $p = 0.328$). Similar to Arakan, individuals with abnormal hermaphroditic gonads were found in each size class = 16 mm-below at percentages of 10 to 23%. Overall, there were no significant differences in the proportions of males, females and 'abnormal' individuals of *N. pullus* between Arakan and Likupang ($\chi^2 = 3.68$, $p = 0.159$).

Table 5.4. Size distribution of sexes in *N. pullus* from Likupang

Shell (mm)	Males	Females	Sex Ratio	c ²	p value	'abnormal'
14	0	2	1.00	-	-	0
15	0	3	1.00	-	-	0
16	3	9	0.75	3.00	0.083	2
17	3	14	0.82	7.12	0.008**	4
18	7	18	0.72	4.84	0.028*	3
19	9	11	0.55	0.20	0.155	6

A total of 103 mature specimens of *N. bimaculosus* from Likupang were analysed. Overall, the number of females was significantly higher than the number of males (Table 5.5: 63 vs. 40; $\chi^2 = 5.14$, $p = 0.023$).

In contrast to *N. pullus*, there were no 'abnormal' hermaphroditic individuals of *N. bimaculosus*. Females were more frequent in August, September and October but the sex ratio did differ significantly from 0.5 only in September ($\chi^2 = 0.73$, $p = 0.039$).

Table 5.5. Monthly distribution of sexes in *N. bimaculosus* from Likupang

Months	Unsexed	Males	Females	Sex Ratio	c ²	p value
August	14	24	38	0.61	3.16	0.075
September	17	7	12	0.63	0.73	0.039
October	16	9	13	0.59	1.32	0.251
Totals	48	40	63	0.61	5.14	0.023*

A similar pattern was found for the distribution of sex ratios across the shell lengths (Table 5.6). There were more females than males throughout the entire size range but this

Table 5.6. Size distribution of sexes in *N. bimaculosus* from Likupang

Shell (mm)	Males	Females	Sex Ratio	c ²	p value
13	2	4	0.67	0.67	0.414
14	6	8	0.57	0.07	0.782
15	15	21	0.58	1.00	0.317
16	12	20	0.63	2.00	0.157
17	5	11	0.69	2.25	0.134

numerical dominance was statistically not significant at any size class between 14 and 17 mm-below due to small sample sizes (χ^2 tests, $p > 0.05$). Not surprisingly, the sex proportions did also not differ significantly among the size classes ($\chi^2 = 0.90$, $p = 0.924$).

5.3.3 Gonad stages

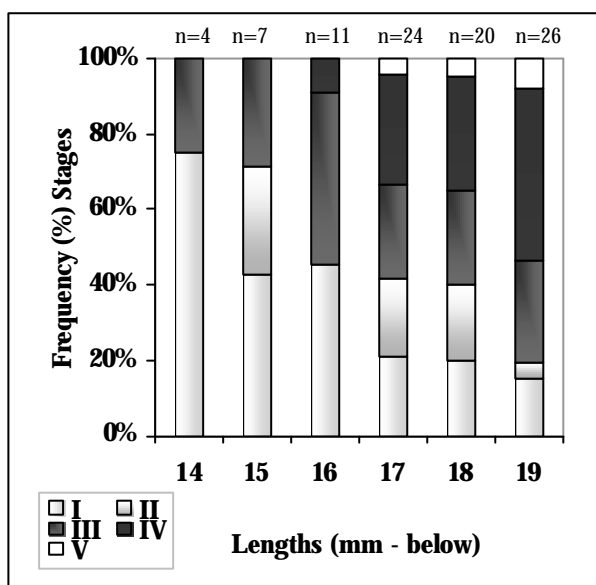
Figure 5.3 shows the distribution of gonad development stages in each size class for *N. pullus* from Arakan and Likupang and *N. bimaculosus* from Likupang. Unsexed (immature) and 'abnormal' hermaphroditic individuals were not included in the computation of proportions.

For *N. pullus* from Arakan, the proportion of sexually active individuals (i.e., those with gonads in stage III or IV) increased dearly with size from approximately 25% at 14 mm-below

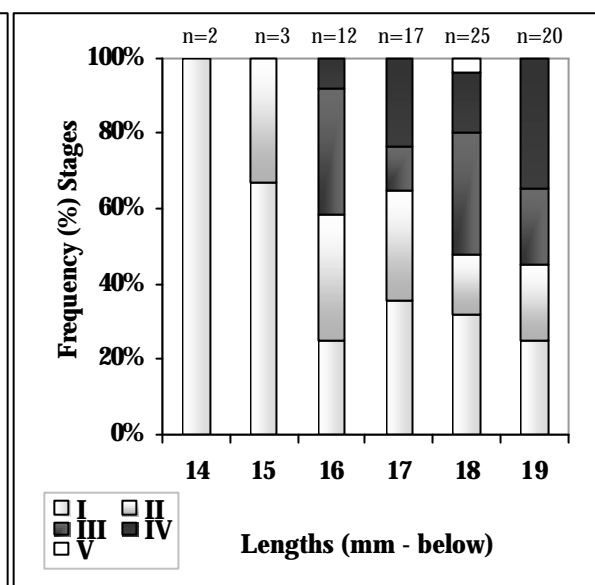
to a maximum of > 70% at 19 mm-below (Figure 5.3a). At Likupang (Figure 5.3b), the first sexually active individuals appeared at a size of 16 mm-below (approximately 40%). Their proportion of the mature population rose to approximately 50% at 19 mm-below.

In *N. bimaculosus* from Likupang (Figure 5.3c), even the smallest mature individuals at a size of 13 mm-below were sexually active (one third featured gonads in stage III). At larger sizes (14 to 17 mm-below), the majority of the mature population (between 50 to 70%) had gonads in a late development or spawning stage (III and IV, respectively) and, hence, could be regarded as sexually active.

a). *N. pullus*, Arakan



b). *N. pullus*, Likupang



c). *N. bimaculosus*, Likupang

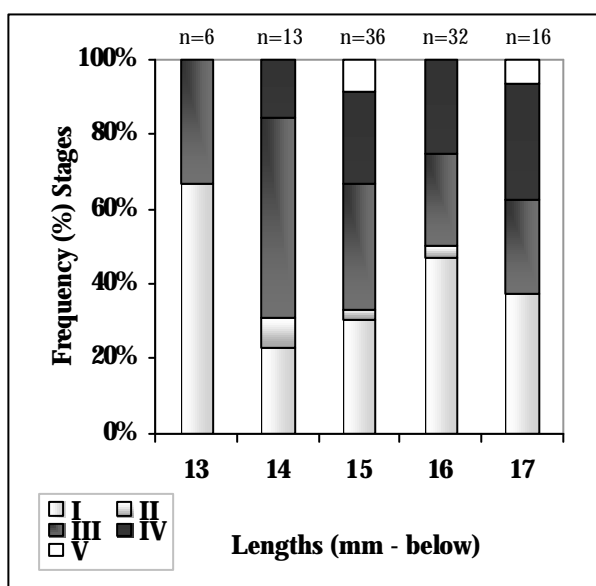


Figure 5.3. Percentage of occurrence of gonad stage in each size class of *N. pullus* from Arakan and Likupang; and *N. bimaculosus* from Likupang. n indicates the number of samples used for microscopic examination of the gonads.

Figure 5.4 shows that *N. pullus* spawns at both Arakan and Likupang in each month during the study period between August and October. At Arakan (Figure 5.4a), the proportion of sexually active individuals in the mature population ranged between 40% in September and about 70% in October, whereas at Likupang (Figure 5.4b) these proportions varied between about 40% in August and about 50% in September. At both Arakan and Likupang, the shares of the sexually active specimens in the mature population fluctuated but there was no clear trend for an increase or a decrease during the 3-month study period.

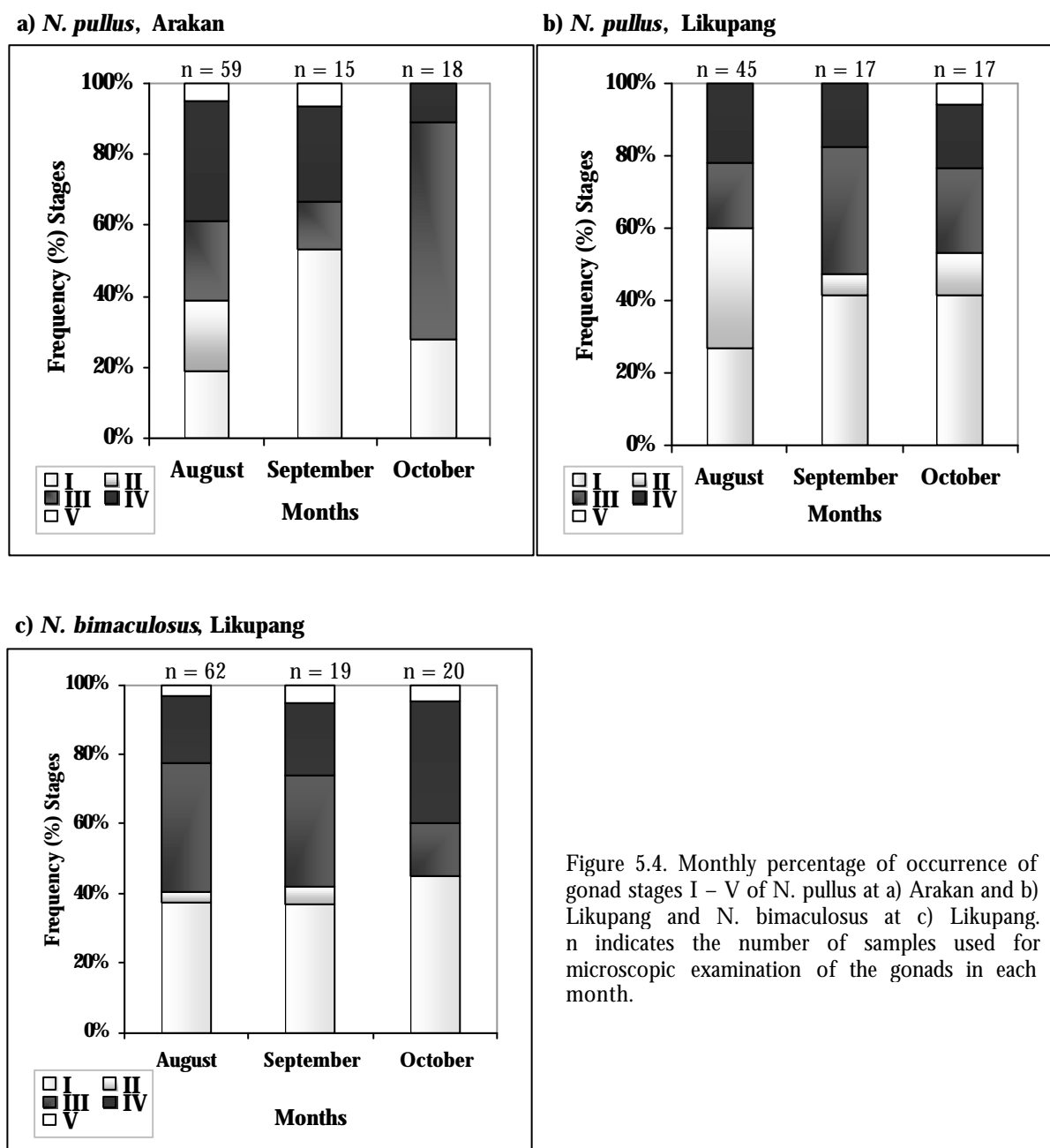


Figure 5.4. Monthly percentage of occurrence of gonad stages I – V of *N. pullus* at a) Arakan and b) Likupang and *N. bimaculosus* at c) Likupang. n indicates the number of samples used for microscopic examination of the gonads in each month.

Also for *N. bimaculosus*, I could find evidence that spawning occurred in each month between August and October (Figure 5.4c). The proportion of sexually active individuals (stage III and IV) were always at level of about 50%, with increasing shares of stage IV gonads and decreasing shares of stage II gonads.

5.4 DISCUSSION

Nassarids differ greatly in the age and size at which they reach maturity. Common species of temperate areas, such as the American mud snail, *N. (= Ilyanasa) obsoletus*, reach maturity at an age of 1.5 to 2 years when the shell reaches a length of 12 mm (Smith, 1980). According to Tallmark (1980), other species from the Gullmar Fjord (Sweden) e.g. *N. reticulatus*, take 3.5 years and shell lengths of 15 mm to mature. Lambeck (1984) found that *N. reticulatus* from Gravelingen (Netherlands) become sexually mature at a shell length of 15 to 16 mm at age 3. Demaintenon (2001a) reported that *N. vibex* from the southeastern part of the United States reach maturity at a shell length of 11.5 mm for males and more than 15.0 mm for females but they gave no information about the growth rate of this species.

Off Northern Minahasa, *N. pullus* reached sexual maturity (L_{50}) at the same size (16 mm-below) at Arakan and Likupang, while *N. bimaculosus* from Likupang had a L_{50} at a smaller shell length (14 mm-below). *N. pullus* reached maturity at a size of 16 mm, while *N. bimaculosus* did at 14 mm. Applying the von Bertalanffy growth (VBG) models (chapter 4.3.2), these sizes equal ages of 1.5 years (18 months) and 1.0 year (12 months), respectively. Based on longevities of 3.85 and 3.00 years, respectively (see chapter 4.3.4), mature *N. pullus* can live for further 2.35 years and mature *N. bimaculosus* for further 2 years.

Of the numerous environmental variables, which potentially influence reproduction in marine invertebrates, sea temperature is assumed to be of highest significance, although for intertidal species, air temperature may be equally important (Seed & Brown, 1977; Tallmark, 1980; Barroso & Moreira, 1998). In temperate zones, seasonal temperature fluctuations are known to be a controlling factor in gametogenesis; however, in tropical areas temperature does not vary much and the critical temperature may change throughout the range of the species (Fretter, 1984).

During my study the variation in environmental parameters were not very pronounced. Temperature ranged between 29 and 33°C and salinity between 33 – 35. Therefore, it is impossible to assess the relationship between temperature and reproduction for *N. pullus* and *N. bimaculosus*.

The intertidal flats off Arakan and Likupang differed in exposure and, hence, probably also food supply for nassariid snails. However, this contrast had apparently no influence on the

size at maturity of *N. pullus*, as the L_{50} lengths did not differ between the exposed Likupang and the sheltered Arakan.

In both *N. pullus* and *N. bimaculosus*, there were some large specimens (= 16 mm-below) that could not be sexed because gonad tissue could not be distinguished in the microscopic preparations. It is very unlikely that these specimens were juveniles. I rather ascribe this finding to two possible reasons: 1) the gonadal tissue was damaged during section and could, hence, not be properly examined under the microscope; 2) the specimens were males with testes in developing stages I or II in which the spermatocytes (which are much smaller than oocytes) are not discernible at the magnifications used.

In general, there are two main results with regard to the sex ratio of the investigated populations: 1) most mature nassariids examined off northern Minahasa were females, and 2) the proportions of females increased with body size (although these general findings were not always statistically significant due to rather small sample sizes). This distribution pattern is typical for most nassariid species (Smith, 1980). It can be caused by different processes, such as differential mortality, differential growth, or ontogenetic sex change (Wright & Lindberg, 1982; Warner, 1988).

At least for *N. pullus*, there is evidence that the latter cause might be of major importance. In contrast to *N. bimaculosus*, a considerable proportion of the larger specimens (= 16 mm-below) had 'abnormal' gonads containing both male and female gametes at both Arakan and Likupang. This can be interpreted as an indication that *N. pullus* is a 'sequential hermaphrodite' in which an individual is first one sex and then changes to the other at some later stage of life. In case of 'protandry', for instance, individuals are first male, then female. Ideally, all individuals below a certain critical size would then be males and all individuals above it females. However, this was not the case for *N. pullus*, as there were some small females and also some large males, at least within the size range I investigated (10 to 19 mm-below). This can be explained by the fact that in protandric species the sex change is usually delayed or omitted in some males for some reason (Warner, 1988). On the other hand, I cannot rule out that the occurrence of 'abnormal' gonads are rather indicating imposex or pseudohermaphroditism in *N. pullus*, caused by an unknown stress factor, as it was reported for several temperate nassariid species (*N. obsoletus*, *N. reticulatus*, *N. vibex*) which are known to actually be strictly dioecious (Smith, 1980; Stroben et al., 1992; Huet et al., 1995; Barroso & Moreira, 1998; Barreiro et al., 2001; Demaintenon, 2001a, 2001b). Further investigations over a longer time span are necessary to decide whether *N. pullus* is a regular protandric hermaphrodite or whether the populations off northern Minahasa comprise a certain proportion of accidental pseudohermaphroditic individuals.

Sequential hermaphroditism is not unusual among gastropods (Fretter, 1984). The sex change-size (or age) hypothesis predicts that sex change has a selective advantage when reproductive success of the two sexes is different with respect to size (or age). For example,

protandry may be favoured if female egg production increases with size while the ability of males to fertilize eggs is independent of size (Warner, 1980; Collin, 1995). The timing of the sex change is affected by a variety of environmental factors that differ among species (Warner, 1988).

The analyses of the gonad development stages yielded basically two main results:

- 1) In both *N. pullus* and *N. bimaculosus*, gametogenesis was not synchronized between the individuals but occurred throughout the entire study period between August and October. Thus, quite high proportions of the mature population were sexually active, indicating that spawning took place, at any time.
- 2) Most female gonads investigated contained gametes at different stages of development, and there were only very few gonads in a 'post-spawning' condition.

The first finding supports the assumption that the nassariids off northern Minahasa spawn throughout the year, as it is typical for tropical species in general (Grahame & Branch, 1985). However, because of the rather short study period I cannot rule out that there is some seasonal variation in spawning activity. A very pronounced seasonal spawning is typical for temperate nassariids, e.g., *N. reticulatus* from Portugal (Barroso & Moreira, 1998), The Netherlands (Lambeck, 1984) or Sweden (Tallmark, 1980), in which spawning is restricted to spring and early summer.

The second finding provides evidence that the nassariids of northern Minahasa are partial spawners, as is also typical for the reproduction of many tropical invertebrates (Fretter, 1984). Such a reproductive adaptation is known to contribute to a prolonged or quasi-permanent spawning.

In the 'abnormal' gonads of *N. pullus*, containing both male and female gametes, the oocytes were always in a later development stage than the spermatocytes. If I assume that *N. pullus* is a sequential hermaphrodite, this pattern can be interpreted as an adaptation in spawning strategy to avoid self-fertilization.

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APPENDIX

Table 1. Average monthly densities (ind m⁻²) of seven nassariid species along tidal gradient at three study sites (Arakan, Mokupa and Likupang) off northern Minahasa, Sulawesi, Indonesia, from August 2000 to July 2001 U = upper zone, M= middle zone and L = lower zone

August 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.5	0.2	0	0	0	0	3.2	1.0	0
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	4.5	2.7	0.3	0	0	1.3	0	0	0
<i>N. luridus</i>	0.0	0	0	0.3	0.1	0	0	0	0
<i>N. pullus</i>	2.6	1.4	0.1	0.1	0.1	0.1	0	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0.2	0	0
<i>H. corticata</i>	2.2	7.5	2	2.3	0	3.6	0	0	0
TOTAL	9.8	11.8	2.4	2.6	0.3	5.0	3.4	1.0	0

September 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.3	0.1	0	0	0	0	3.9	2.1	0.1
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	2.9	1.6	0	1.4	0.8	0	0	0	0
<i>N. luridus</i>	0.4	0	0	0.4	0.6	0.1	0	0	0
<i>N. pullus</i>	2.9	0.1	0	0.1	0	0	0.1	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0	5.5	3.0	4.9	4.0	0.4	0	0	0
TOTAL	6.5	7.4	3.0	6.8	5.4	0.5	4.0	2.1	0.1

October 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.3	0.2	0	0	0	0	2.6	1.2	0
<i>N. camellus</i>	0	0.0	0	0	0	0	0	0	0
<i>N. globosus</i>	0.8	0.4	0.4	0.6	0	0	0	0	0
<i>N. luridus</i>	0	0.1	0	1.0	0	0	0	0	0
<i>N. pullus</i>	2.0	0.7	0	0.3	0	0	0	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0.7	3.4	2.1	2.1	0.8	0	0	0	0
TOTAL	3.7	4.7	2.6	4.0	0.8	0	2.6	1.2	0

Tabel 1 continued

November 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.3	0.3	0	0	0	0	3.6	1.8	0.3
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	2.3	2.6	0	0.1	0.5	0	0	0	0
<i>N. luridus</i>	0	0.1	0	1.0	2.1	0.8	0	0	0
<i>N. pullus</i>	2.3	0.9	0	0.5	1.0	0.1	0.8	0.1	0
<i>N. venustus</i>	0	0	0	0	0	0	0.5	0	0
<i>H. corticata</i>	0.6	1.7	2.7	3.6	3.8	0	0	0	0
TOTAL	5.5	5.5	2.7	5.3	7.4	0.9	4.9	1.9	0.3

December 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.6	0.6	0	0	0	0	4.1	1.3	0.3
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	4.9	3.7	0	1.4	1.4	0.3	0	0	0
<i>N. luridus</i>	0.3	0.7	0	2.6	1.8	2.0	0	0	0
<i>N. pullus</i>	3.3	1.6	0.1	0.1	0.1	0.6	0.2	0.3	0
<i>N. venustus</i>	0	0	0	0	0	0	0.3	0	0
<i>H. corticata</i>	0.3	4.9	1.7	6.3	1.5	0.1	0	0	0
TOTAL	9.3	11.5	1.9	10.4	4.8	3.0	4.6	1.6	0.3

January 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.8	0.5	0	0	0	0	2.6	2.4	0.2
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	4.2	2.9	0	3.8	0.5	0	0	0	0
<i>N. luridus</i>	0.1	0	0	1.8	1.9	0	0	0	0
<i>N. pullus</i>	2.8	1.5	0	1.1	0.1	0	0.3	0.2	0.1
<i>N. venustus</i>	0	0	0	0	0	0	0.6	0	0
<i>H. corticata</i>	1.0	4.0	1.9	5.4	4.5	0	0	0	0
TOTAL	8.9	8.9	1.9	12.0	7.0	0	3.6	2.6	0.3

February 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	1.6	0.4	0	0.1	0.6	0	3.6	1.6	0
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	2.3	2.5	1.0	0.4	0.8	0	0	0	0
<i>N. luridus</i>	0.1	0	0	2.3	0.5	0.3	0	0	0
<i>N. pullus</i>	4.3	1.0	0.1	1.1	0.3	0	0.4	0.1	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0	4.3	1.5	0.6	1.5	0	0	0	0
TOTAL	8.3	8.2	2.6	4.5	3.6	0.3	4.0	1.7	0

Tabel 1 continued

March 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.3	0	0	0.9	0.1	0	3.0	2.1	0.3
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	3.8	3.8	0	0.3	0.4	0.1	0	0	0
<i>N. luridus</i>	0	0.1	0	1.4	0.6	0	0	0	0
<i>N. pullus</i>	2.4	0.7	0	0.9	0	0	0.3	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0.4	0	0
<i>H. corticata</i>	0.5	4.9	1.5	0	0.1	0	0	0	0
T O T A L	7.1	9.8	1.5	3.4	1.3	0.1	3.7	2.1	0.3

April 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.5	0.8	0	0	0.1	0	1.8	0.6	0.2
<i>N. camellus</i>	0	0.3	0	0	0	0	0	0	0
<i>N. globosus</i>	4.3	5.1	0.7	0.3	0.8	0	0	0	0
<i>N. luridus</i>	0.1	0.3	0	1.8	0.4	0	0	0	0
<i>N. pullus</i>	1.9	1.8	0.1	0.4	0	0	0	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0.3	0	0
<i>H. corticata</i>	0.1	1.7	1.9	0.3	1.0	0	0	0	0
T O T A L	6.8	10.0	2.8	2.6	2.3	0	2.1	0.6	0.2

May 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.4	0	0	0	0.3	0	1.8	0.7	0
<i>N. camellus</i>	0.2	0.5	0.2	0	0	0	0	0	0
<i>N. globosus</i>	1.1	3.1	0.9	1.6	1.1	0	0	0	0
<i>N. luridus</i>	0.2	1.1	0.1	2.4	1.4	0.4	0	0	0
<i>N. pullus</i>	1.6	0.7	0	0	0	0	1.3	0.5	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0	1.6	2.3	1.6	0	0	0	0	0
T O T A L	3.5	7.0	3.6	5.6	2.8	0.4	3.1	1.2	0

June 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.1	0	0	0.3	0	0	0.9	1.0	0.2
<i>N. camellus</i>	0.8	2.4	0	0	0	0	0	0	0
<i>N. globosus</i>	1.3	1.6	0	2.5	2.0	0	0	0	0
<i>N. luridus</i>	0.1	0	0	1.9	1.0	0	0	0	0
<i>N. pullus</i>	2.1	1.4	0	0	0	0	0.7	0.5	0.3
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0	1.1	1.8	0.9	0.1	0	0.3	0	0
T O T A L	4.3	6.5	1.8	5.5	3.1	0	1.9	1.5	0.5

Tabel 1 continued

July 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.1	0	0	0	0	0	2.4	0.7	1.0
<i>N. camellus</i>	1.4	1.3	0	0	0	0	0	0	0
<i>N. globosus</i>	2.0	0.9	0	2.0	0.6	0.1	0	0	0
<i>N. luridus</i>	0.1	0.1	0	2.0	0.8	0	0	0	0
<i>N. pullus</i>	2.5	0.5	0	0	0	0	1.7	0.6	0.6
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0.3	1.9	1.5	1.0	0	0	0.2	0	0
TOTAL	6.4	4.7	1.5	5.0	1.4	0.1	4.3	1.2	1.6

Table 2. Average monthly biomass (mg AFDW m⁻²) of seven nassariid species along tidal gradient at three study sites (Arakan, Mokupa and Likupang) off northern Minahasa, Sulawesi, Indonesia, from August 2000 to July 2001 U = upper zone, M= middle zone and L = lower zone

August 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.4	0	0	0	0	0	57.8	6.8	0
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	40.4	9.1	0	0	0	1.6	0	0	.0
<i>N. luridus</i>	0	0	0	0.4	0.1	0	0	0	0
<i>N. pullus</i>	50.1	14.8	0.2	0.2	0.1	0	0	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0.9	0	0
<i>H. corticata</i>	6.8	97.0	3.6	15.7	0	20.0	0	0	0
TOTAL	97.8	120.9	3.7	16.2	0.2	21.6	58.6	6.8	0

September 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	1.1	0.3	0	0	0	0	109.7	28.8	0.1
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	63.6	19.5	0	3.3	1.1	0	0	0	0
<i>N. luridus</i>	6.0	0	0	0.9	2.7	0.1	0	0	0
<i>N. pullus</i>	178.3	0.2	0	0.3	0	0	0.1	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0	100.1	30.7	121.4	108.8	1.5	0	0	0
TOTAL	249.1	120.1	30.7	125.9	112.5	1.6	109.8	28.8	0.1

October 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.6	0.3	0	0	0	0	24.8	6.4	0
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	5.5	1.2	0.8	0.6	0	0	0	0	0
<i>N. luridus</i>	0	0.1	0	10.0	0	0	0	0	0
<i>N. pullus</i>	32.6	3.3	0	0.5	0	0	0	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	3.3	178.5	19.0	13.4	0.9	0	0	0	0
TOTAL	42.0	183.4	19.9	24.4	0.9	0	24.8	6.4	0

Tabel 2 continued

November 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.6	1.1	0	0	0	0	123.5	13.9	0.1
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	34.5	41.1	0	0.6	0.3	0	0	0	0
<i>N. luridus</i>	0	0	0	10.6	15.5	2.6	0	0	0
<i>N. pullus</i>	53.4	9.0	0	12.6	2.1	0.1	41.9	1.2	0
<i>N. venustus</i>	0	0	0	0	0	0	5.3	0	0
<i>H. corticata</i>	0.2	1.0	1.9	28.5	10.5	0	0	0	0
T O T A L	88.7	52.3	1.9	52.3	28.4	2.7	170.6	15.0	0.1

December 2000

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	2.2	1.4	0	0	0	0	241.3	29.6	0.9
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	62.3	41.0	0	7.4	9.6	0.4	0	0	0
<i>N. luridus</i>	0.9	5.6	0	47.8	31.7	25.0	0	0	0
<i>N. pullus</i>	59.6	38.9	0.1	0.1	0.5	2.6	0.4	2.8	0
<i>N. venustus</i>	0	0	0	0	0	0	1.4	0	0
<i>H. corticata</i>	0.1	39.9	5.0	101.3	6.5	0	0	0	0
T O T A L	125.1	126.8	5.1	156.6	48.2	28.0	243.1	32.5	0.9

January 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	1.8	0.7	0	0	0	0	120.1	105.4	0.6
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	90.7	54.5	0	80.3	5.6	0	0	0	0
<i>N. luridus</i>	0.1	0	0	89.8	110.1	0	0	0	0
<i>N. pullus</i>	207.8	78.2	0	0.6	0.2	0	1.0	0.5	0
<i>N. venustus</i>	0	0	0	0	0	0	10.2	0	0
<i>H. corticata</i>	7.9	218.8	52.2	180.1	135.9	0	0	0	0
T O T A L	308.4	352.2	52.2	350.7	251.7	0	131.3	105.9	0.6

February 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	18.4	0.7	0	0.1	2.7	0	164.7	26.8	0
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	34.0	54.1	4.9	1.7	3.2	0	0	0	0
<i>N. luridus</i>	0.4	0	0	45.2	2.2	0.5	0	0	0
<i>N. pullus</i>	357.1	19.7	0.2	176	0.5	0	6.5	0.5	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0	193.3	26.8	2.5	11.9	0	0	0	0
T O T A L	409.9	267.9	31.9	67.1	20.4	0.5	171.2	273	0

Tabel 2 continued

March 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.3	1.2	0	6.7	0.2	0	107.4	63.3	1.3
<i>N. camellus</i>	0	0	0	0	0	0	0	0	0
<i>N. globosus</i>	141.7	73.3	0	2.6	6.1	0.1	0	0	0
<i>N. luridus</i>	0	0.2	0	18.4	3.3	0	0	0	0
<i>N. pullus</i>	91.4	7.5	0	9.9	0	0	4.1	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	2.4	184.0	19.9	0	0.2	0	0	0	0
T O T A L	235.9	266.3	19.9	37.5	9.7	0.1	111.5	63.3	1.3

April 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	1.4	1.2	0	0	0.3	0	34.5	3.7	0.2
<i>N. camellus</i>	0	0.4	0	0	0	0	0	0	0
<i>N. globosus</i>	121.2	154.5	2.8	1.2	3.9	0	0	0	0
<i>N. luridus</i>	0.1	0.5	0	47.1	2.5	0	0	0	0
<i>N. pullus</i>	49.1	45.9	0.3	2.2	0	0	0	0	0
<i>N. venustus</i>	0	0	0	0	0	0	0.9	0	0
<i>H. corticata</i>	0	27.0	13.7	0.3	9.4	0	0	0	0
T O T A L	171.8	229.5	16.9	50.8	16.1	0	35.4	3.7	0.2

May 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.4	0	0	0	0.3	0	15,8	1,7	0
<i>N. camellus</i>	0.1	1.6	0	0	0	0	0	0	0
<i>N. globosus</i>	5.5	52.4	3.3	22.4	7.1	0	0	0	0
<i>N. luridus</i>	0.1	13.9	0	49.4	17.1	1.1	0	0	0
<i>N. pullus</i>	32.0	7.8	0	0	0	0	8.1	0.7	0
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0	13.0	17.2	30.6	0	0	0	0	0
T O T A L	38.1	88.6	20.6	102.4	24.5	1.1	23.8	2.4	0

June 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0	0	0	0.3	0	0	12.8	15.5	0.7
<i>N. camellus</i>	1.4	11.8	0	0	0	0	0	0	0
<i>N. globosus</i>	6.7	11.5	0	68.3	41.2	0	0	0	0
<i>N. luridus</i>	0	0	0	50.3	12.7	0	0	0	0
<i>N. pullus</i>	56.3	21.8	0	0	0	0	6.0	2.2	0.8
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0	5.2	11.4	3.9	0.1	0	1.1	0	0
T O T A L	64.6	50.3	11.4	122.7	54.0	0	19.9	17.7	1.5

Tabel 2 continued

July 2001

	Arakan			Mokupa			Likupang		
	U	M	L	U	M	L	U	M	L
<i>N. bimaculosus</i>	0.7	0.	0	0	0	0	67,2	4.5	9.3
<i>N. camellus</i>	3.8	2.5	0	0	0	0	0	0	0
<i>N. globosus</i>	14.2	3.3	0	7.2	0.6	0	0	0	0
<i>N. luridus</i>	0	0	0	26.6	4.1	0	0	0	0
<i>N. pullus</i>	79.8	2.7	0	0	0	0	30.8	1.6	3.3
<i>N. venustus</i>	0	0	0	0	0	0	0	0	0
<i>H. corticata</i>	0.4	12.7	18.4	2.6	0	0	0.3	0	0
TOTAL	98.9	21.2	18.4	36.4	4.8	0	98.3	6.0	12.6

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- 1984** Graduated from High School in Ambon, Indonesia.
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