Seasonality of marine algae and grazers of an Antarctic rocky intertidal, with emphasis on the role of the limpet *Nacella concinna* Strebel (Gastropoda: Patellidae)

Dohong Kim

- To my mother and father -
for patiently waiting so long

Dohong Kim
Polar Research Center
Korea Ocean Research & Development Institute
Ansan P.O.Box 29
Seoul 425-000
Korea

Contents

Glossary

ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
d.f.	Degrees of freedom
ind.	Individual
M.H.W.N.	Mean high water of neap tides
M.L.W.N.	Mean low water of neap tides
max	Maximum
min	Minimum
n	Total number of replicates
nd	No data available
SE	Standard error
st.	Station
Σ	Total

Abstract

The seasonal change in abundance and distribution of intertidal algae and the interaction between algae and Antarctic limpets *Nacella* (*Patinigera*) *concinna* (Strebel, 1980) were studied in the rocky intertidal of King George Island, South Shetland Islands, during two austral summers and one austral winter. Furthermore, the seasonal pattern of ice disturbances and its influence on the development of algae were investigated.

Most intertidal algal species are annual and pseudo perennial and exhibit large fluctuations in abundance and distribution with intertidal shore levels and season, as well as interannual variations. Nevertheless, a rough zonation of macroalgae was recognisable: the upper intertidal is characterised by *Porphyra endiviifolium* and *Urospora penicilliformis*, the middle by *Adenocystis utricularis* and *Iridaea cordata* with *Monostroma hariotii*, and the lower intertidal fringe by lithothamnioid and some sublittoral macroalgae. Most intertidal algae (*M. hariotii*, *Palmaria decipiens*, *Acrosiphonia arcta*, filamentous algae), which were abundant during the first summer, did not occur during the second summer.

Disturbance by ice foot occurred in winter, while ice scouring by floating ice was severe before forming and after receding of sea ice. Intensity and frequency of disturbances by ice foot and ice scouring increased with increasing shore levels. Except for the upper intertidal, however, the percentage cover of the annual algae did not decrease with increasing shore levels. In addition, most algae disappeared from the intertidal before the formation of ice foot. On the other hand, the density of the pseudo perennial macroalga *Adenocystis utricularis* was negatively impacted by the disturbance of ice foot.

Mark-recapture experiments and distribution of limpets indicated that the important grazer *Nacella concinna* migrated seasonally from the sublittoral to the littoral in summer. Since limpets reduced the density of filamentous algae and of the diatom film during the upward migration, herbivore grazing limits the distribution of Antarctic intertidal algae at low shore levels, while physical ice disturbance controls algal growth at the upper shore levels. The relative effects of *N. concinna* on the marcoalgae appeared to be severe in early life stages compared to adults. In the first summer, upward migration of limpets was delayed by high

densities of green algae, whereas the lack of green algae in the second summer forced limpets to migrate rapidly to the intertidal.

A significant difference in shell heights of limpets was found between the intertidal and sub-littoral groups. In addition, mark-recapture experiments showed a significant difference in migratory behaviour between the two groups, indicating that the intertidal migrants appeared to be adapted morphologically and physiologically to the intertidal habitat. On the other hand, the intertidal limpets exhibited a strong bias to females (male:female, 1:1.359) and mean shell size in males was significantly larger than in females, while the sex ratios in sublittoral limpets were approximately 1:1. Furthermore, only adult limpets (> 20 mm) were found in the intertidal. It can be presumed that the population characteristics in the Antarctic limpet are largely different between the intertidal and sublittoral sub-population.

A significant decrease of limpet gonad condition factors was noted between January and February 1997 reflecting the liberation of gametes during this period. Due to the absence of food between November and December 1997, the somatic condition factor of limpets decreased dramatically. In contrast, the gonad condition factor continuously increased during the second summer. Thus, it can be inferred that *Nacella concinna* is more flexible in growth rate rather than reproduction with respect to the fluctuation of food availability.

Zusammenfassung

Im Rahmen dieser Arbeit wurden die jahreszeitlichen Unterschiede in der Abundanz und Verteilung der Algen in der Gezeitenzone und die Wechselwirkungen zwischen Algen und der antarktischen Napfschnecke *Nacella* (*Patinigera*) *concinna* (Strebel, 1980) untersucht. Zudem wurden die saisonale Auswirkung der Eisstörungen und deren Einfluß auf die Entwicklung der Algen untersucht. Die Arbeiten fanden an einer Felsküste der King-George-Insel, Süd-Shetland-Inseln, während zweier Sommer und eines Winters statt.

Die meisten Algenarten im Gezeitenbereich sind annuell und pseudoperennierend, und ihre Abundanz zeigte große saisonale Schwankungen. Ihre Dichte und Arten-zusammensetzung änderten sich vom ersten zum zweiten Jahr. Trotz der Schwankungen war eine grobe Zonierung im Gezeitenbereich erkennbar: *Porphyra endiviifolium* mit *Urospora penicilliformis* waren im oberen, *Adenocystis utricularis* und *Iridaea cordata* mit *Monostroma hariotii* im mittleren, und Kalkalgen und einige sublitorale Algenarten im unteren Gezeitenbereich vorhanden. Die meisten Algen (*M. hariotii, Palmaria decipiens, Acrosiphonia arcta*, filamentöse Algen), die im ersten Sommer stark verbreitet waren, kamen im zweiten Sommer nicht vor.

Während das Eulitoral im Winter durch den an das Festlandeis anschließenden "Eisfuß" (engl. ice foot) gestört wurde, wirkt sich das Kratzen und Pflügen schwimmenden Eises kurz vor der Bildung und nach dem Aufbrechen der Meereisdecke stark auf den Gezeitenbereich aus. Die Intensität und Häufigkeit der Eisstörungen nahmen mit zunehmender Strandhöhe zu. Außer im oberen Gezeitenbereich nahm der prozentuale Bedeckungsgrad der annuellen Algen mit zunehmender Gezeitenhöhe jedoch nicht ab. Außerdem verschwanden die meisten litoralen Algenarten vor der Bildung des Eisfußes. Zudem wurde die Dichte der pseudoperennierenden Makroalge *Adenocystis utricularis* durch die Störung des Eisfußes negativ beeinflußt.

Ein Markierungsexperiment und die Verteilungen der als Weidegänger bedeutsamen Napfschnecken machen es wahrscheinlich, daß *Nacella concinna* im Sommer vom Sublitoral zum Eulitoral wanderte. Die Dichte der filamentösen Algen und des

Diatomeenfilms ging während der Aufwärtswanderung der Napfschnecken zurück. Daher ist anzunehmen, daß die Abundanz und Verteilung der eulitoralen Algen im unteren Gezeitenbereich durch das Abweiden der Herbivoren beeinflußt wurde, während die physikalischen Eisstörungen das Wachstum der Algen im oberen Gezeitenbereich kontrollierten. Anscheinend wirkt sich das Weiden der Napfschnecken stärker auf die frühen als auf die adulten Stadien der Makroalgen aus. Die Aufwärtswanderung wurde durch den dichten Bewuchs von Grünalgen im ersten Sommer verzögert, während das Fehlen von Grünalgen im zweiten Sommer zu einer schnellen Wanderung in den oberen Gezeitenbereich führte.

Ein signifikanter Unterschied der Schalenhöhen der Napfschnecken wurde zwischen der eulitoralen und der sublitoralen Untergruppe gefunden. Außerdem zeigte das Markierungsexperiment einen signifikanten Unterschied im Wanderungsverhalten der beiden Gruppen. Die in die Gezeitenzone wandernden Napfschnecken scheinen sich morphologisch und physiologisch dem litoralen Habitat anzupassen. Es wurden mehr weibliche als männliche Napfschnecken gefunden (männlich:weibliche 1:1,359), und die mittlere Schalengröße der männlichen Napfschnecken war signifikant größer als die der weiblichen. Das Geschlechterverhältnis der sublitoralen Napfschnecken war dagegen annähernd 1:1. Interessanterweise wurden nur Adulte (> 20 mm) im Eulitoral gefunden. Aus diesen Ergebnissen kann abgeleitet werden, daß die Populationsmerkmale antarktischer Napfschnecken für die eulitorale and sublitorale Subpopulation unterschiedlich sind.

Eine signifikante Abnahme des Konditionsfaktors der Gonaden zwischen Januar und Februar 1997 deutet darauf hin, daß die Reproduktion der Napfschnecken während dieses Zeitraums stattfand. Ohne Nahrung zwischen November und Dezember 1997 sank der somatische Konditionsfaktor dramatisch. Im Gegensatz dazu nahm der Gonaden-konditionsfaktor im zweiten Sommer ununterbrochen zu. Daraus kann gefolgert werden, daß die Wachstumsrate von *N. concinna* flexibler als ihre Reproduktion in bezug auf die Schwankungen in Nahrungsangebot reagiert.

Chapter 1

General introduction

Previous work and problem

Antarctic and sub-Antarctic rocky intertidal assemblages have been described in a number of publications (Knox 1960, Delépine et al. 1966, Zaneveld 1966, Hedgpeth 1969, 1971, Gruzov and Puskin 1970, Stockton 1973, 1990, Arnaud 1974, DeLaca and Lipps 1976, Moe and DeLaca 1976, Petrov and Nikolaev 1982, Ramirez and Villouta 1984, Castilla and Rozbaczylo 1985, Zielinski 1990, Gallardo et al. 1999). Most of them describe vertical zonation patterns in a narrative way in qualitative terms only.

From these reports, the intertidal zone of the Antarctic appears to be inimical to living organisms (for a review see Arntz et al. 1994, Clarke 1996). Ice is an important factor controlling distribution and occurrence of intertidal organisms (for a review see Barnes 1999). For example, the intertidal zone is heavily disturbed by snow and ice foot in winter (Delépine et al. 1966, Walker 1972, Shabica 1972, 1976), allowing macroalgae only to overwinter in form of rhizoidal crusts or spores (sensu Heywood and Whitaker 1984). Additionally, floating sea ice may scour parts of the intertidal also during summer (e.g., Neushul 1966, Hedgpeth 1969, Barnes 1995, Pugh and Davenport 1997). On the other hand, the ice cover during winter may prevent exposure of the tide pools to low air temperatures (Shabica 1972, Walker 1972). This protection effect of the ice thus may permit an overwintering of algae between tidemarks (Shabica 1972). Indeed, some observations (Gutkowski and Maleszewski 1989, Klöser pers. comm.) indicate that at least some species may remain intact opposite to previous opinions. When the sea-ice cover disappears from the rocky shore, algae and diatoms quickly develop and attain a considerable biomass (Hedgpeth 1971, Stockton 1973, Arnaud 1974, Castilla and Rozbaczylo 1985, Zielinski 1990, for a review see Dayton 1990). Even in summer, sessile marine invertebrates are largely absent, and the only animals in the intertidal found in quantity are limpets (Hedgpeth 1969, Shabica 1971, 1976, Walker 1972, Castilla and

Rozbaczylo 1985, Brêthes et al. 1994) and motile amphipods (Jazdzewski et al. 1986, Rauschert 1991).

Unfortunately, few papers focus on the dynamics of coastal ecosystems or on the mechanisms explaining the above mentioned patterns of vertical distribution (i.e. for Antarctic shallow sublittoral environments see Dayton et al. 1974). Generally speaking, there is a rudimentary scientific knowledge about trophic structure of these assemblages on Antarctic coasts and a lack of experimental work (Castilla and Rozbaczylo 1985). Particularly, it remains largely unknown to which degree Subantarctic and Antarctic rocky intertidal assemblages are biologically or physically accommodated.

The limpet *Nacella* (*Patinigera*) *concinna* (Strebel, 1908) in particular is a partial herbivore, grazing microphytobenthos (Shabica 1976, Brand 1980, Iken 1995), calcareous rhodophytes (Brand 1980), and seaweed (Iken 1995), but also on bryozoans and sessile spirorbid polychaetes (Brand 1980). In summer, it is abundant in the intertidal as well as in the sublittoral (Walker 1972, Shabica 1976, Brêthes et al. 1994).

It is not clear, what factor triggers the immigration of limpets into the intertidal in spring. Competing explanations are: density dependent migration to evade intraspecific competition, attraction by the availability of an important alternative energy resource due to the growth of benthic microalgae in the intertidal, and an internal behavioural trigger mechanism in the postulated migratory sub-population (Walker 1972, Brêthes et al. 1994). As during winter the animals are forced to withdraw from the then frozen intertidal, they may migrate back into the sublittoral in autumn (Walker 1972, Shabica 1976, Brêthes et al. 1994), thereby increasing the grazing pressure on sublittoral algae. Low air temperatures are considered to be the essential trigger for this downward migration (Walker 1972). However, *Nacella concinna* is the prime prey of the kelp gull *Larus dominicanus* (Hedgpeth 1969, Shabica 1976, Castilla and Rozbaczylo 1985, Favero et al. 1997, 1998, Silva 1999). Hedgpeth suggested that the limiting factor for the intertidal occurrence of *N. concinna* may be predation by gulls rather than ice abrasion.

Nacella concinna spawns once a year during the Austral summer in the shallow sublittoral with external fertilisation (Shabica 1971, 1976, Picken 1980, Picken and Allen 1983, Brêthes et al. 1994, Stanwell-Smith and Clarke 1998). Spawning coincides with raising water temperature (Shabica 1971, Picken 1980, Picken and Allen 1983, Brêthes et al 1994) and may be related to increasing spring food availability (Brêthes et al 1994, Stanwell-Smith and Clarke 1998). Judging from this, reproduction in the intertidal seems to be improbable. Whether this is true, is not known. Assuming that it is true, a further question would be, whether animals living in the intertidal may not become fertile, or whether they migrate back to the sublittoral for reproduction.

Questions

In this study, I attempted to answer the following main questions:

• When and where do which marine algae occur in the Antarctic intertidal?

• Which factors (physical vs. biological disturbance) are important for controlling the distribution and abundance of intertidal algae?

• Which factors control the population structure of *Nacella concinna*?

• How can the fluctuation of food availability influence the life history of *Nacella concinna*?

Approach and outline of thesis

To answer the first and second question I followed the phenomenology of the intertidal marine organisms during two austral summers and one austral winter (Chapter 3). In addition, the distribution and abundance of the intertidal algae and *Nacella concinna* were quantified in a selected intertidal area. In order to answer the second question these quantified data for the intertidal algae were related to the occurrence of the physical (ice impact) and biological (grazing by *N. concinna*) disturbances. To answer the third question I described seasonal changes in the population structure of the intertidal *Nacella concinna* (Chapter 4). In addition, this chapter provides the migratory behaviour of *N. concinna* and predation by kelp gull *Larus dominicanus*, which may be a key factor for maintaining the

population structure of the intertidal limpet population. Finally, the reproduction of *Nacella concinna* in relation to food availability is treated in Chapter 6. General conclusions integrating the results of this and other studies and an outlook on further directions are provided in Chapter 7.

Chapter 2

Study area

Geographical situation and topography

King George Island is the largest island of the South Shetland Islands, which is situated approximately 100 km from the Antarctic Peninsula. The study area is about 2.5 km from the Korean research station (King Sejong, 62° 13′S, 58° 47′W) on Barton Peninsula which is situated at the north-eastern side of Maxwell Bay, one of two large fjords in King George Island, facing south-easterly to Bransfield Strait. Two tributary basins, Marian and Potter Cove, are situated in both sides of Barton Peninsula. Most part of this study was performed on the south-west tip of Barton Peninsula, which is moderately exposed to the oceanic swells and wave action from the Bransfield Strait. It was chosen for this study because the shore is typical of the range from volcanic rock platforms to vertical cliffs in the area while the greater part of the coast at Barton Peninsula is pebble or sandy beach (KORDI, 1988).

Hydrography of Maxwell Bay

The general hydrography of the Maxwell Bay is well understood through fairly extensive studies (Heywood 1985, Chang et al. 1990). In the Bransfield Strait two distinctive water masses appear at the surface: relatively warm, less saline water masses originating from the Bellingshausen sea and colder, more saline water from the Weddell Sea. Maxwell Bay is a fjord characterised by a deep sill and relatively small amount of freshwater input. Because Maxwell Bay opens its mouth directly to the Bransfield Strait, surface water originating from the Bellingshausen sea enters into the southern side of the bay, from Bransfield Strait, and flows in a couple of tributary bays (Colins Bay, Marian Cove, Potter Cove) of the northern side before flowing out of the bay.

Ice condition

Sea-ice formation is highly variable at King George Island, due to its position at the edge of the Weddell/Scotia Confluence zone (Murphy et al. 1995, Kang et al. 1997). In 1989, 1983 and 1996 no persistent ice cover occurred in Marian Cove and Maxwell Bay (Kang et al. 1997). In the winter 1997, sea-ice covered Marian Cove, Potter Cove and a part of Maxwell Bay from July to September. An ice foot formed in the intertidal and disappeared later than the sea-ice. Floating ice occurred in summer and was less
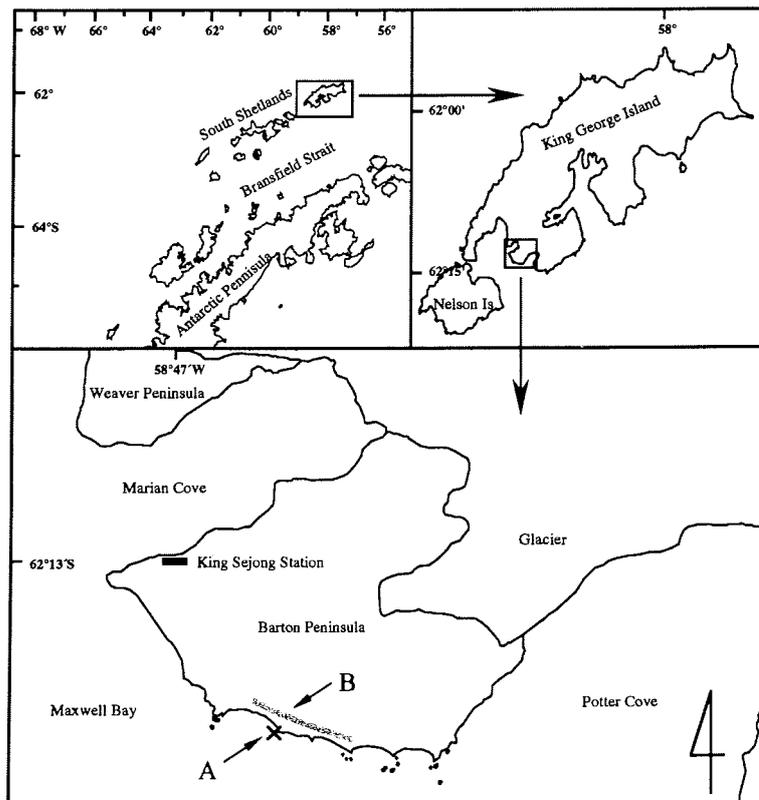
Fig. 2.1. Map of the study area. A: Sites for transect and descriptive studies. B: Sampling site for the regurgitated pellets by the kelp gulls.

biological and physical disturbances on the distribution and abundance of the intertidal algae, a quantitative study was conducted in a selected intertidal area. By examining the influence of ice impact, the distribution and abundance of intertidal algae were related to the various types of disturbance. Biological disturbance was studied as a correlation between *Nacella concinna* densities and the percentage cover of algal species. Furthermore, to quantify variation between years, I compared the phenology of two vegetation periods, the summer of 1996/97 and 1997/98.

3.2. Material and methods

Ice disturbance

In the Maxwell Bay and Marian Cove, formation and presence of sea ice and ice foot were documented during the study period. After the formation of fast ice, holes were cut in the ice in the intertidal and disturbance by the ice foot was recorded. In order to measure the probability of disturbances of ice scouring, 50 nails were embedded into 40 x 20 x 2 cm (thick) wooden plates, which were installed at two different intertidal levels (at M.L.W.N. and M.H.W.N.). Each nail stood approximately 2 cm high. After two days the bent and missing nails were counted and recorded as "nail mortality" (compare with Dayton 1971). The measurements were carried out during spring tides only.

Vertical distribution of intertidal algae and grazers

The study was carried out during two austral summers and one austral winter, from November 1996 to March 1998. Two sites (a horizontal, flat rocky shore and a vertical cliff) were selected for the descriptive studies. Algae and invertebrates were collected, their vertical positions and relative abundances were recorded. The organisms were preserved in formalin for identification. Colour photographs were taken and later used to check the levels reached by characteristic organisms.

One middle intertidal rocky platform was selected where quadrat sampling was performed for the quantitative survey of seasonal patterns of distribution of algae and limpets. At the end of November 1996, seven stations along a transect line in a distance of 4 m were marked perpendicular to the water from mean low water neap tide (M.L.W.N.) to mean high water neap tide (M.H.W.N., representing station 1 in tables and figures) just above the upper limits of limpets in summer. Within each of these stations, a series of randomly placed, replicate quadrats was sampled within 5 m on either side of the transect.

A 50 x 50 cm quadrat was used for the counting of *Nacella concinna*. This procedure was replicated 8 times at each station from December 1996 to October 1997 and again 32 times from November 1997 to February 1998. Point quadrat sampling (Foster et al. 1991, Fig. 3.1 a) was performed in order to determine percentage cover of macroalgae. This procedure was replicated 6 times at each station during the first summer and 8 times during the second summer. Two 40 x 40 x 0.7 cm (thick) plexiglass plates were held parallel by three stainless legs. The plates were perforated by a grid of 100 holes. The holes were 4 mm in diameter, spaced at 3 cm intervals in a 30 x 30 cm area within the plate. The percent cover of algae was estimated by passing a sharpened, 4 mm diam. stainless steel rod through the upper and lower hole. The rod passed through the holes of two parallel plates
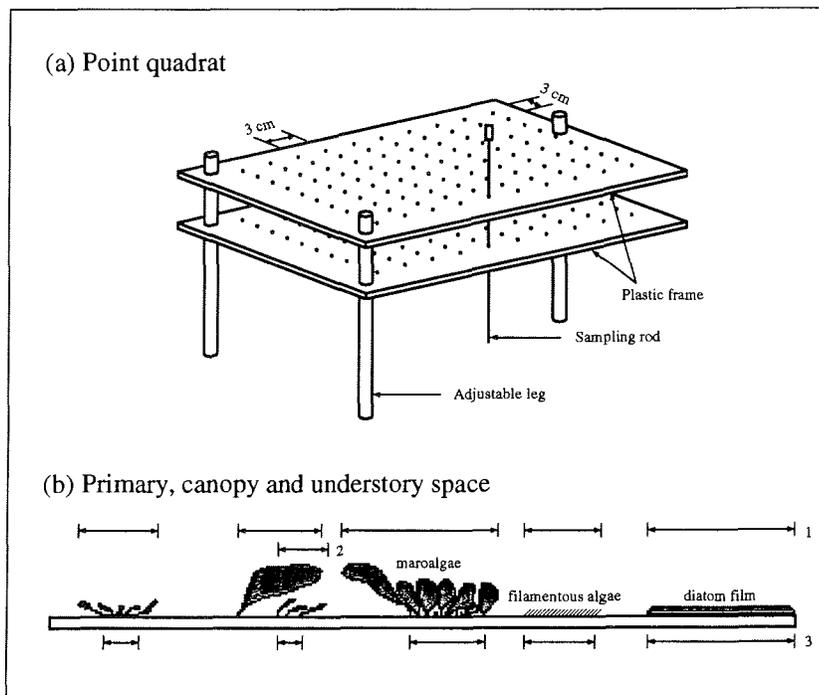
Fig. 3.1. Construction of point quadrat (a), and diagrammatic view (b) of canopy (1), understory (2) and primary space (3).

and did not move horizontally. Thirty holes were chosen at random for the percent cover of algae. Each alga which was contacted by the tip of the rod was recorded. When layering occurred, upper layers were recorded at first, then moved aside, and the rod lowered down to the next contact and so forth, so the multiple contacts under a single point of different taxa (canopy-understorey space). The primary space, such as holdfasts of macroalgae, bare rock and diatom film, was recorded (3.1 b). Total cover, the sum of the cover of all taxa, thus could exceed 100. Rock-pools, however, were not sampled. Whenever a pool deeper than 20 cm was encountered, quadrats were moved sideways from the line of the transect to avoid it.

Statistics

To compare the disturbance of ice scouring between the different months or the different sites, non-parametric methods of analysis were used because the variances of "nail mortality" were unequal after the angular transformation; the Mann-Whitney U test for the difference between the upper and lower intertidal and Kruskal-Wallis Test for the difference between the different months.

All statistical comparisons of percent cover data were performed on values normalized with an arcsine transformation (Sokal and Rolf 1969). After data from station 1 to 7 were pooled, one-way ANOVAs (effect: month, 11) on percent cover were employed for the seasonal changes in the intertidal algae and bare space. Furthermore, the data of primary space of *Adenocystis utricularis* and *Iridaea cordata* from December to February were analysed with a three-way ANOVA (effect: year, month, station, 2 x 3 x 7) because of their regular occurrence. Two-way ANOVA (effect: month, station, 11 x 7) was performed for the seasonal and vertical change of *Nacella concinna*. Post-hoc comparisons were done according to Tukey-Kramer and with mean comparisons (*t*-Test).

To examine the effect of ice foot on the intertidal algae, the primary spaces of *Adenocystis utricularis* and *Iridaea cordata* at the ice foot zone (Station 1 to 4) and the zone below the ice foot (Station 5 to 7) were compared before the formation (May 1997) and after receding of ice foot (October 1997) by a two-way ANOVA (effect: ice foot, zone, 1 x 1).

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For the effect of grazing on the intertidal algae, linear regressions between density of *Nacella concinna* and primary space of intertidal algae were performed. Data of *Nacella concinna* were log-transformed (log (x +1)).

3.3. Results

3.3.1. General patterns of distribution in the intertidal

General patterns of distribution and seasonal occurrence of macroalgae are summarised in Figure 3.2. In general, in the rocky intertidal of Barton Peninsula perennial macroalgae and sessile animals were absent, except for the lowest intertidal. The distribution of organisms in the intertidal could be divided in three major zones.

The upper intertidal was characterised by disturbance of ice foot and ice scouring. Grazers, such as *Nacella concinna* and *Naevilittorina* sp., were absent. In general, on the flat shore macroalgae were absent and bare space was very abundant. On the vertical rock (Fig. 3.3) there was a zone predominantly occupied by the red alga *Porphyra endiviifolium* with filamentous algae, such as *Urospora penicilliformis*, *Ulothrix* sp. and *Bangia atropurpurea*, whose distribution extended down into the middle intertidal. *Enteromorpha* sp. together with diatoms occurred in rock pools and crevices in the upper intertidal belt.

The middle intertidal was most disturbed by a high spatial and temporal variability. On vertical rocks, filamentous algae occurred in the whole middle intertidal in spring, but rapidly disappeared during summer. On the flat shore (Fig. 3.4) the green algae *Monostroma hariotii* and filamentous green algae spread very quickly as soon as the ice foot disappeared in spring. The red alga *Palmaria decipiens* inhabitated the rock pools. In the lower part of the middle intertidal, thalli of *Adenocystis utricularis* and *Iridaea cordata* were growing occasionally in rock crevices and at edges of the shallow pools. In January, the green alga *Acrosiphonia arcta* was observed in the region which was undisturbed by grazers. The macroalgal grazer, *Nacella concinna*, migrated in this zone and grazed on green algae during summer (Fig. 3.5). In addition, numerous small gastropods, e.g. *Naevilittorina* sp., inhabited crevices depressions, whereas turbellarians were situated under boulders and in shallow pools.

(a) Seasonal changes
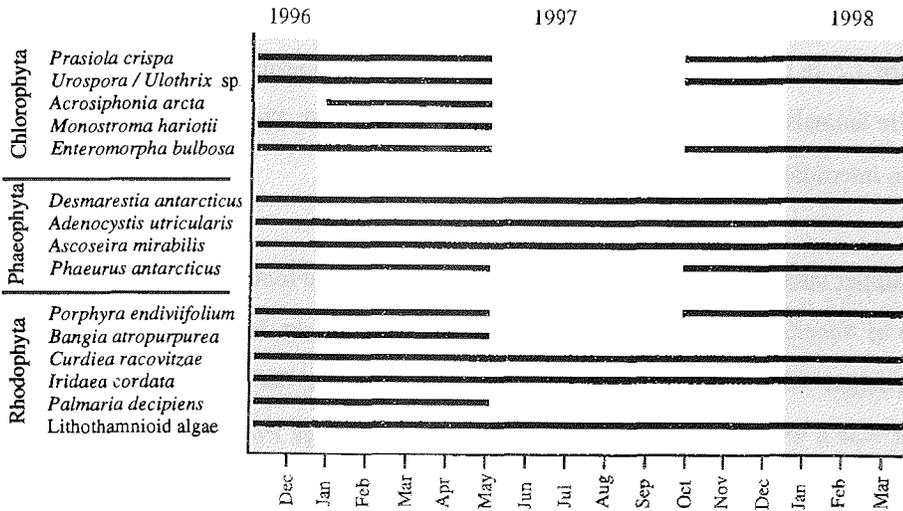
(b) Vertical distribution
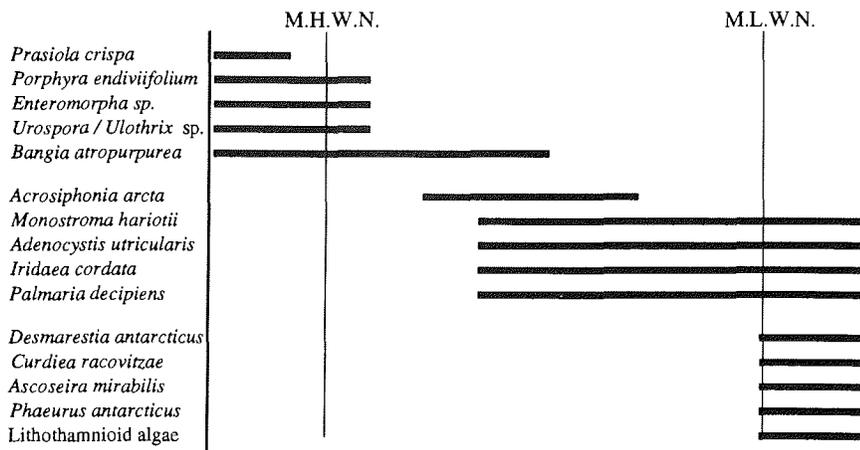
Fig. 3.2. Seasonal changes (a) and vertical distribution (b) of intertidal marine algae at King George Island.

The lower intertidal was characterised by the absence of ice foot in winter and occurrence
of *Nacella concinna* throughout the year. *Adenocystis utricularis* and *Iridaea cordata*
mainly were observed all year round. The annual green alga *Monostroma hariotii* and the
red alga *Palmaria decipiens* were found occasionally in summer, but not in high quantities.
A few sessile species, the hydrozoan *Silicularia rosea* and some molluscs, attached to the
sides of boulders. In the lowest part of the intertidal the macroalgae *Ascoseira mirabilis*,
Gigartina skottsbergii, *Phaeurus antarcticus* and *Desmarestia* sp., occurred in rock pools
and extended down to the sublittoral.
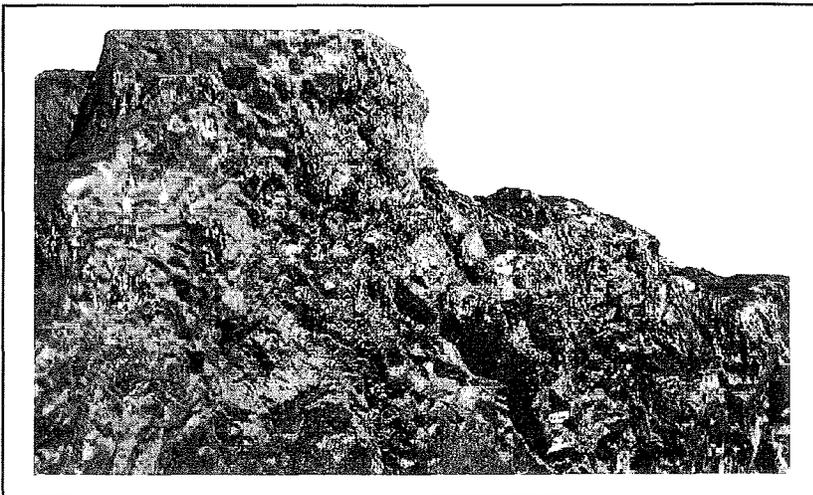
Fig. 3.3. Spring bloom of *Porphyra endiviifolium* with filamentous algae in the upper intertidal on vertical
rock.

Fig. 3.4. Spring mass bloom of *Adenocystis utricularis*, *Monostroma hariotii* and *Palmaria decipiens* in the mid-intertidal of a flat shore.
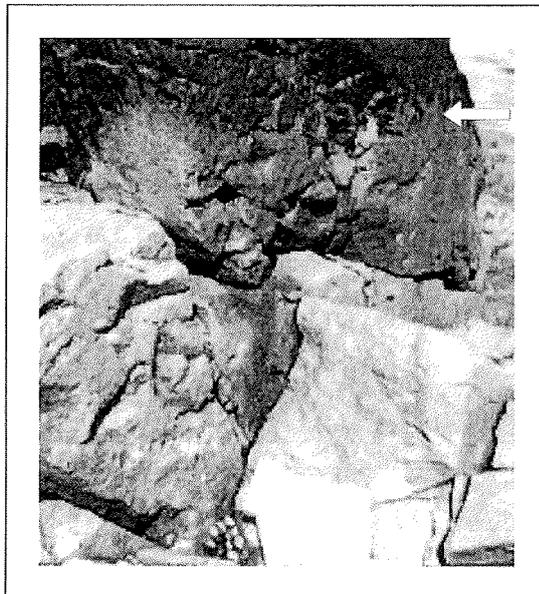
Fig. 3.5. Grazing of *Nacella concinna* on filamentous algae. Arrow indicated border beween grazed (below) and ungrazed (above) surface.

3.3.2. Seasonal changes of distribution in the middle intertidal

3.3.2.1. Ice disturbance

An ice foot was formed in the intertidal from July to September, but its duration and extension varied with the profile of the substrate. On a steep shore it extended from extreme high water spring tides to extreme low water spring tides, covering the whole intertidal (Fig. 3.6). On a less steep shore in the intertidal a lot of pancake ice was beached, remaining gaps were covered by snow (Fig. 3.7). The size of beached pancake ice depended on the tidal level and increased from upper to lower intertidal (about 2 – 3 m height at sampling site). As a consequence, in the lower intertidal (at station 5, 6 and 7) there were nets of ice tunnels in between the pancake ice which were connected to the sublittoral, while ice encased the whole surface of the upper intertidal.

Ice scouring by floating ice occurred only in summer. The experiment of nail "mortality" (Fig. 3.8) showed that ice scouring by floating ice varied with season (Kruskal-Wallis Test, $P < 0.001$). Ice scouring was severe just before and after the formation of fast ice, whereas
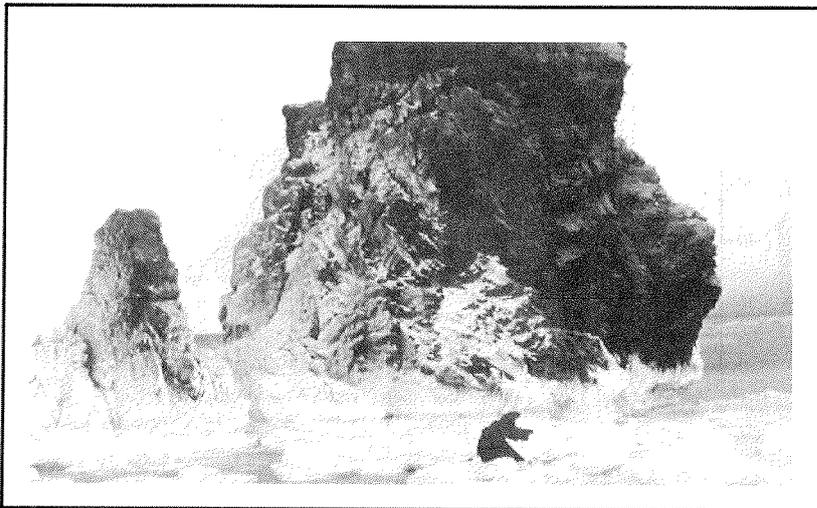
Fig. 3.6. Ice foot on a vertical rock.

it was less from December to February. The upper part of the mid-intertidal was significantly more disturbed by ice scouring in comparison to the lower part of the mid-intertidal (Mann-Whitney U test, $P < 0.001$). Thus, the disturbance by ice foot and ice scouring showed high seasonality and variation in tidal levels.
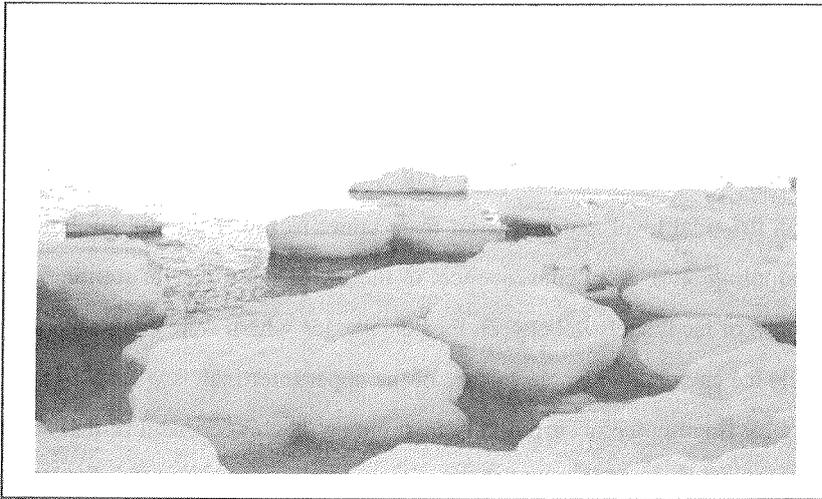
Fig. 3.7. Pancake ice on a flat shore.
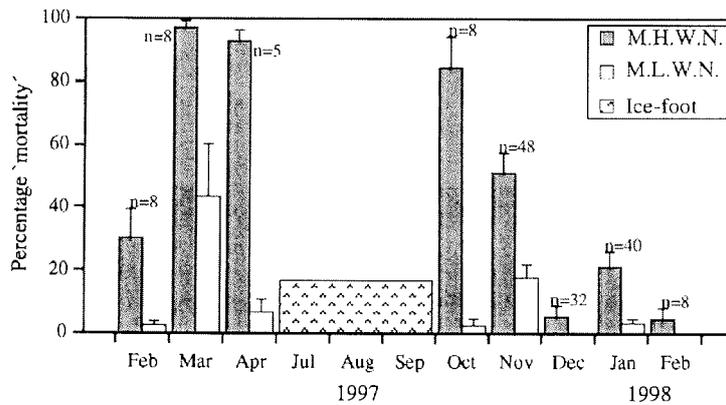
Fig. 3.8. Percentage "mortality" of nails by ice scouring with numbers of replicates from January 1997 to February 1998. Vertical bars represent one standard error. n: total number of wooden plates.

3.3.2.2. Density and distribution of *Nacella concinna*

Nacella concinna entirely disappeared from the intertidal in winter and recolonised again in summer, indicating seasonal migration. If the data of density from Station 1 to 7 are pooled, the mean density in the intertidal varied from 0 in July 1997 to 47 ± 3.2 ind. / m² in February 1998 (Fig. 3.9). The maximal mean density was 129 ± 49.5 SE ind. / m², found at station 4 in February 1997.

Fig. 3.10 shows the seasonal changes in the vertical distribution of *N. concinna*. Upward migration began just after receding of the ice foot in October and mean density rapidly increased until January. From January to February, mean density did not change ($t_{1,110} = 0.064$, $P > 0.05$ in the first summer; $t_{1,446} = 1.009$, $P > 0.05$ in the second summer). From
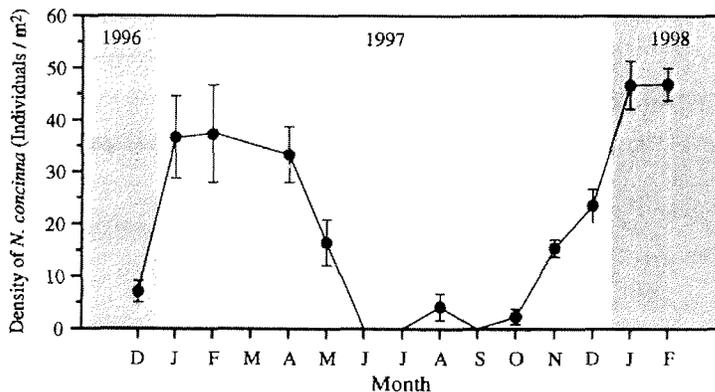
Fig. 3.9. Seasonal changes of mean densities with standard error of *Nacella concinna* in the middle intertidal of King George Island from December 1996 to February 1998.

Fig. 3.10 (next page). Seasonal changes of vertical distribution of *Nacella concinna* and ice cover in the middle intertidal of King George Island from December 1996 to February 1998. Density with one standard error of *Nacella concinna*. Station 1 is situated at M.H.W.N. and station 7 at M.L.W.N..
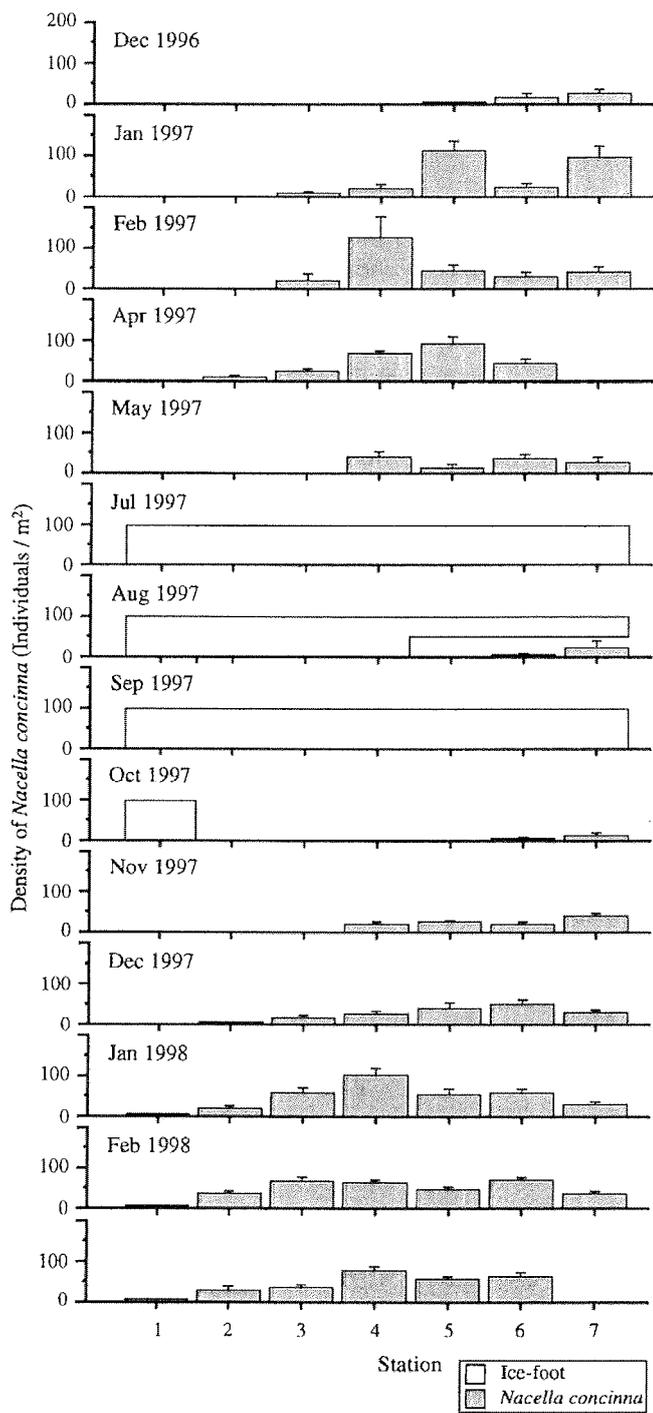
April onward, limpet numbers decreased until no limpets were found that were air exposed at low tide at the end of May. During the formation of ice foot in winter, *Nacella concinna* occasionally migrated upwards, depending on weather condition and stretch of ice foot in the intertidal (e.g. August in Fig. 3.10). At the study site, the upper limit of the distribution of *Nacella concinna* was higher in the second summer (station 2 in December 1997) than in the first summer (station 5 in December 1996). Although more limpets, on the whole, migrated in the first summer than in the second summer, there was no significant difference in the mean densities between the two summers ($t_{1,278} = 0.986$, $P > 0.05$ in January; $t_{1,278} = 1.182$, $P > 0.05$ in February).

3.3.2.3. Marine algae and bare space

The mean number of algal species was low. In only two sampling periods (December 1996 and January 1997) the number of species exceeded four per quadrat and this occurred only at station 3 and 4. Except for *Adenocystis utricularis* and *Iridaea cordata*, most algae occurred only in the first summer, and their distribution was restricted to the middle and upper part of the sampling area. *A. utricularis*, *I. cordata* and *Porphyra endiviifolium* were observed just before the formation of ice foot, whereas the other species entirely disappeared earlier from the intertidal. Patterns of allocation of primary and canopy-understorey space over the whole period of this study showed large variations with season (Table 3.1 and 3.2).

Bare space is very abundant along the studied transect, but it varied with months and tidal levels. Bare space tended on the whole to be less abundant in spring and to increase in the course of summer (Table 3.2). In the summer 1996/97, bare space usually attained values over 80 % at the lower part of the transect, but it was strongly reduced with increasing tidal levels (Fig. 3.11). Bare space increased from April 1997 and values higher than 70 % along the whole transect were recorded. In comparison to the first summer, a negative

Table 3.1. Monthly changes of canopy-understorey space in the summer 1996/97 (a) and 1997/98 (b). Data were pooled from station 1 to 7 and analysed with one-way ANOVA. The table shows the mean percentage cover and its standard error. All data were transformed by the angular transformation.

(a) Summer 1996/97

Month	Dec. 96	Jan. 97	Feb. 97	Apr. 97	May. 97	F, 4 d.f.	
No. quadrats sampled	42	42	42	42	42		
Adenocystis utricularis	17.1 ± 2.0	18.0 ± 2.3	18.7 ± 2.6	15.6 ± 2.1	10.7 ± 1.7	2.2	ns
Iridaea cordata	11.2 ± 2.4	3.2 ± 1.2	3.5 ± 1.3	2.3 ± 1.0	3.8 ± 1.2	5.8	***
Palmaria decipiens	12.2 ± 2.5	3.8 ± 1.0	1.0 ± 0.5	0	0	17.6	***
Monostroma hariotii	30.6 ± 4.1	15.9 ± 2.0	9.2 ± 1.7	2.8 ± 0.9	0	30.6	***
Acrosiphonia arcta	0	3.7 ± 1.2	3.6 ± 1.1	2.8 ± 1.0	0.3 ± 0.3	4.8	***
Porphyra endiviifolium	0	0.3 ± 0.3	0.7 ± 0.5	6.8 ± 1.7	1.8 ± 0.7	10.5	***

(b) Summer 1997/98

Month	Oct. 97	Nov. 97	Dec. 97	Jan. 98	Feb. 98	F, 4 d.f.	
No. quadrats sampled	56	56	56	56	56		
Adenocystis utricularis	5.5 ± 1.2	7.2 ± 1.4	8.3 ± 1.7	9.1 ± 1.6	10.6 ± 1.7	1.6	ns
Iridaea cordata	7.0 ± 1.4	6.9 ± 1.5	5.3 ± 1.1	5.3 ± 1.3	5.5 ± 1.3	0.4	ns
Monostroma hariotii	0	0.2 ± 0.2	0	0	0	1.0	ns

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns not significant, $P > 0.05$.

Table 3.2. Monthly changes of primary space in the summer 1996/97 (a) and 1997/98 (b). Data were pooled from station 1 to 6 and analysed with one-way ANOVA. The table shows the mean percentage cover and its standard error. All data were transformed by the angular transformation.

(a) Summer 1996/97

Month	Dec. 96	Jan. 97	Feb. 97	Apr. 97	May. 97	F, 4 d.f.	
No. quadrats sampled	42	42	42	42	42		
Adenocystis utricularis	15.9 ± 1.9	14.1 ± 2.0	13.9 ± 2.4	11.9 ± 1.8	9.1 ± 1.6	1.8	ns
Iridaea cordata	5.1 ± 1.3	1.9 ± 0.8	2.8 ± 1.1	1.6 ± 0.7	1.5 ± 0.7	2.6	*
Palmaria decipiens	2.7 ± 1.0	0	0	0	0	7.4	***
Monostroma hariotii	9.1 ± 1.8	1.0 ± 0.6	0.3 ± 0.3	0.8 ± 0.4	0	18.9	***
Acrosiphonia arcta	0	3.0 ± 0.9	3.6 ± 1.1	2.5 ± 0.9	0.3 ± 0.3	4.8	*
F + D	24.2 ± 4.7	32.1 ± 4.6	22.7 ± 5.1	8.8 ± 2.0	0	11.5	***
Bare space	45.7 ± 3.4	45.6 ± 3.8	52.0 ± 4.7	69.8 ± 2.3	79.5 ± 1.6	21.1	***

(b) Summer 1997/98

Month	Oct. 97	Nov. 97	Dec. 97	Jan. 98	Feb. 98	F, 4 d.f.	
No. quadrats sampled	56	56	56	56	56		
Adenocystis utricularis	2.4 ± 0.8	2.6 ± 0.8	4.8 ± 1.0	4.8 ± 1.0	5.2 ± 1.0	2.2	ns
Iridaea cordata	3.0 ± 0.8	3.1 ± 0.8	4.1 ± 0.9	3.8 ± 0.9	3.9 ± 1.0	0.3	ns
Diatoms	39.2 ± 2.7	22.7 ± 2.5	0.4 ± 0.3	0	0	114.0	***
Bare space	49.2 ± 2.9	64.4 ± 2.6	82.5 ± 1.3	83.0 ± 1.3	82.3 ± 1.3	57.2	***

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns not significant, $P > 0.05$.

F + D: filamentous algae and diatoms
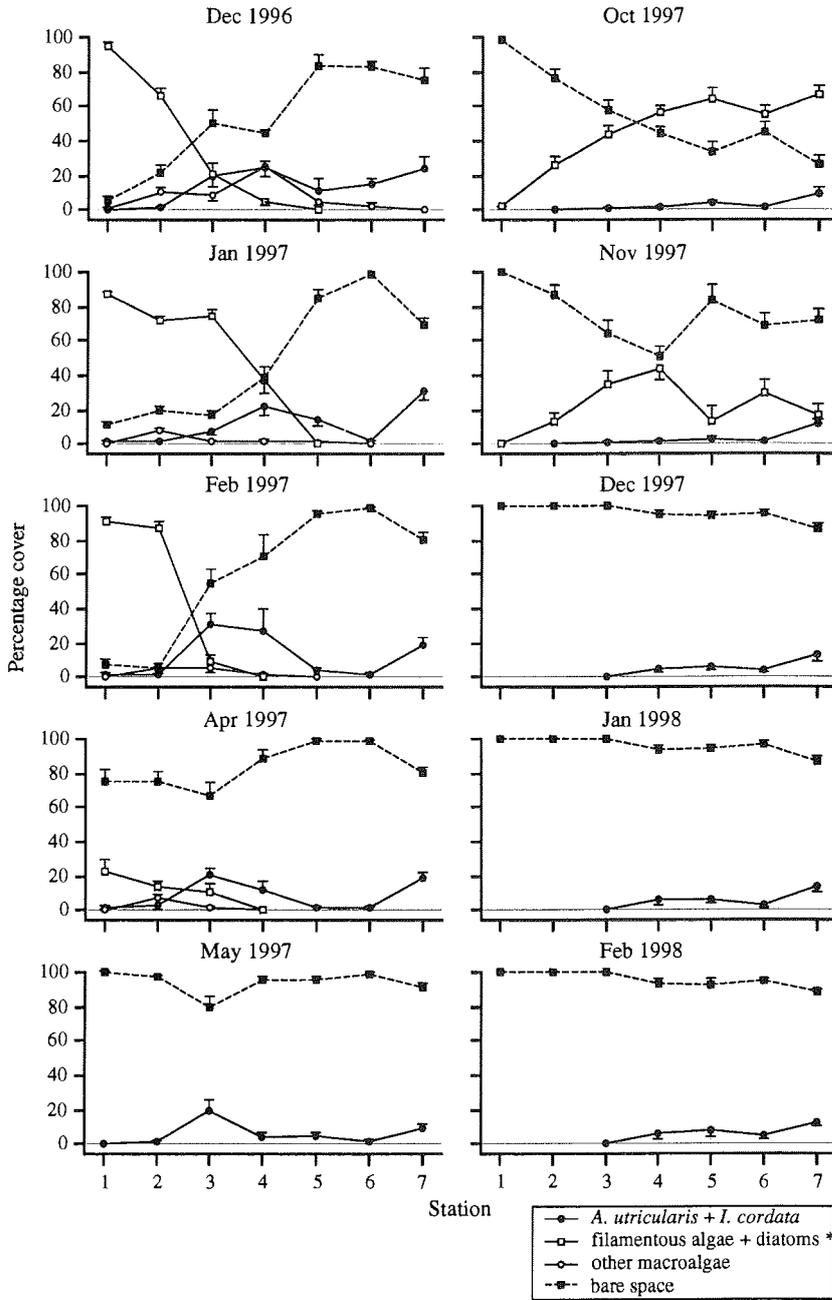
Fig. 3.11. Vertical change of the intertidal algae and bare space in the middle intertidal of King George Island from December 1996 to February 1998. Percentage covers with one standard error of primary space. Station 1 occurs in M.H.W.N. and station 7 in M.L.W.N.. *: diatom film only from October to November 1997.

relationship between bare space and tidal levels was recorded in October 1997. From December 1997, however, it rapidly expanded along the whole transect and reached values over 90 % of the primary space. In compare to the first summer, bare space was remarkably abundant during the second summer.

The fluctuation of <u>filamentous algae and diatom film</u> seems primarily to be responsible for the variation of bare space. In the summer 1996/97, filamentous algae (*Bangia atropurpurea* and *Urospora penicilliformis*) together with diatoms, occupied on average more than 90 % of the primary space in the upper part of the sampling area (Fig. 3.11). Their lower limits moved upwards until February 1997, although the percentage cover increased constantly. After a peak in February filamentous algae gradually disappeared. On the other hand, the filamentous algae were not observed during the summer 1997/98. In October 1997, the diatom film occurred in the whole intertidal, but entirely disappeared in December.

Monostroma hariotii appeared in the intertidal just after receding of ice foot at the end of October 1996. *M. hariotii* grew fast and its length reached ca. 20 cm in January. The distribution of *M. hariotii* extended over the whole transect in December 1996, but the maximum abundance was recorded at the middle level of the sampling area (mean primary space = 18.9 % and mean canopy-understorey space = 91.7 %, Fig. 3.12 and 3.13). The abundance decreased despite an unchanged distribution from January to April. *M. hariotii* completely disappeared before the formation of ice foot in May 1997 (Fig. 3.12). In the summer 1997/98, a few of small germlings were observed in low intertidal pools in November but entirely disappeared in December.

Palmaria decipiens occurred together with *Monostroma hariotii* in the early summer and its length reached over 40 cm in December 1996. The abundance was greater at the middle level of the sampling area in December 1996 (mean primary space = 5.5 % and mean canopy-understorey space = 48.9 %, Fig. 3.12 and 3.13) and it declined rapidly. The distribution of intertidal *P. decipiens* seems to be restricted only in intertidal pools or in the
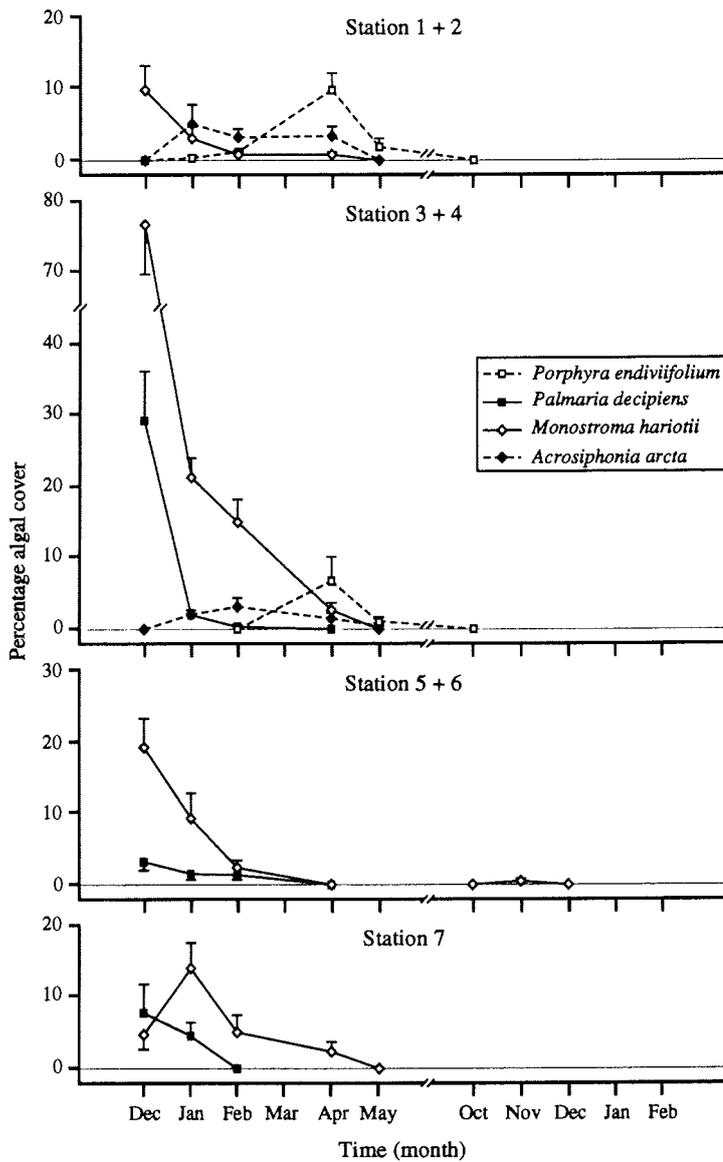
Fig. 3.12. Seasonal change of *Porphyra endiviifolium*, *Palmaria decipiens*, *Monostroma hariotii* and *Acrosiphonia arcta* in the middle intertidal of King George Island from December 1996 to February 1998. Percentage covers with one standard error of canopy-understorey space. Station 1 is situated at M.H.W.N. and station 7 at M.L.W.N..
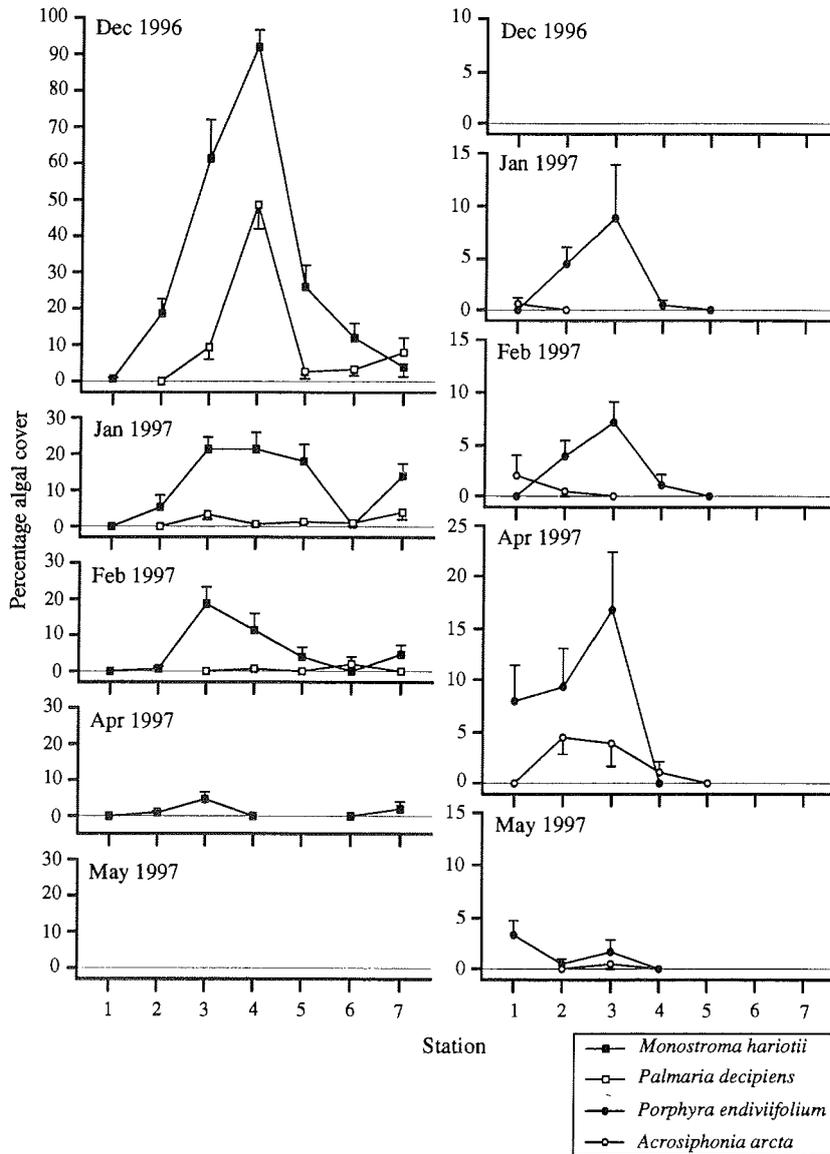
Fig. 3.13. Vertical distribution of *Monostroma hariotii, Palmaria decipiens, Porphyra endiviifolium* and *Acrosiphonia arcta* in the middle intertidal of King George Island from December 1996 to May 1997. They did not occur in the summer 1997/98. Percentage covers with one standard error of canopy-understorey space. Station 1 is situated at M.H.W.N. and station 7 at M.L.W.N..

moist mat of *M. hariotii*. *P. decipiens* entirely disappeared from the intertidal before April 1997 and it was not observed during the second summer.

Distribution of *Porphyra endiviifolium* is usually restricted only in the upper intertidal. In January 1997, however, small blades of *P. endiviifolium* grew in the upper part of sampling area (Fig. 3.12 and 3.13). *P. endiviifolium* was present just before the formation of the ice foot, but it was not observed after receding of the ice foot in October 1997. In the summer 1997/98, although *P. endiviifolium* grew in the upper intertidal of a vertical cliff, it was not observed in the transect.

Acrosiphonia arcta were first seen in the upper part of the sampling area in January 1997 (Fig. 3.12 and 3.13). Distribution of *A. arcta* was restricted to the upper part of the sampling area and its percentage cover rarely exceeded 15 % of canopy-understorey space. *A. arcta* disappeared in May 1997 and did not return in the summer 1997/98.

Adenocystis utricularis was present during the whole period of sampling (Fig. 3.14 and 3.15). Neither during the summer 1996/97 nor during the summer 1997/98 there were significant differences in its percentage cover between months (Table 3.1 and 3.2). It was also observed under the fast ice in the lower intertidal where ice foot did not form during the winter 1997. *A. utricularis* probably developed directly from the microthalli after receding of the ice foot. The germlings of *A. utricularis* were observed at the end of November 1996 and at the end of January 1997. In the summer 1996/97, *A. utricularis* was present over the whole transect. Percentage covers were positively correlated with tidal levels in December 1996, but decreased in station 5 and 6 from January 1997 onwards. This distribution pattern was constant until May 1997, although abundance decreased during autumn. In the summer 1997/98 vertical distribution and abundance of *A. utricularis* were approximately constant during the sampling period.

The data of primary and canopy space of *Adenocystis utricularis* were analysed with a three-factor ANOVA (year, month and zone) because of their regular occurrence during the sampling period (Table 3.3). There were no significant differences between the months from December to February, whereas the percentage cover of the first summer was
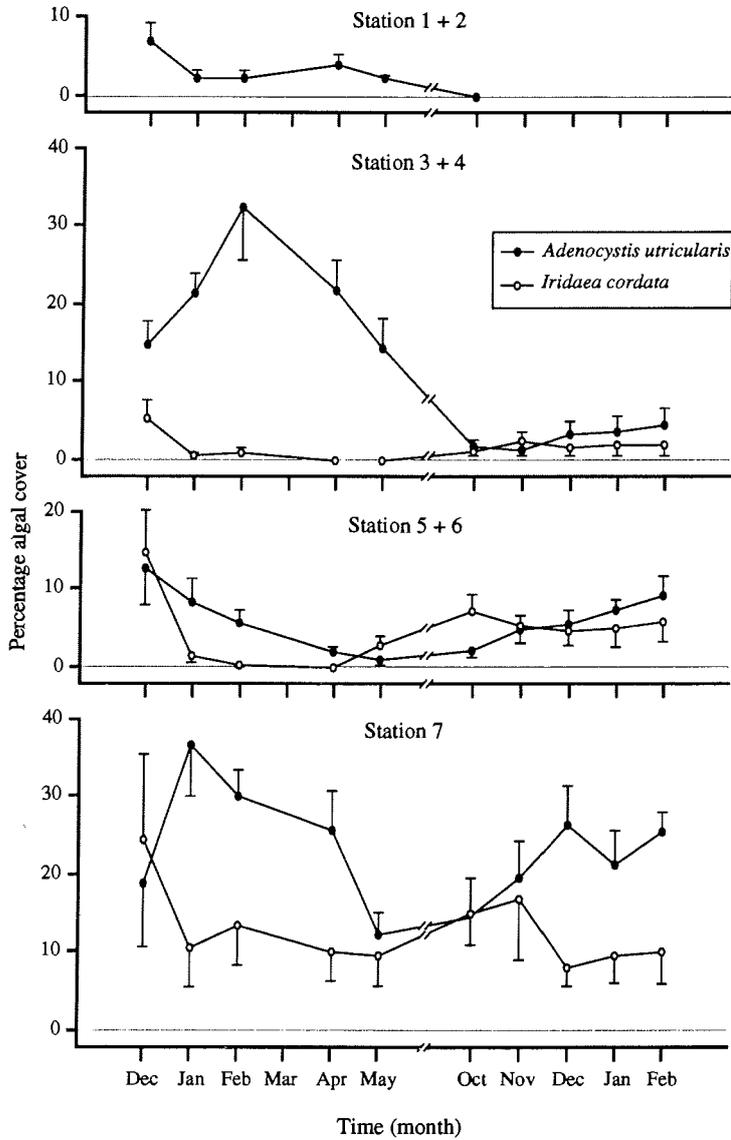
Fig. 3.14. Seasonal change of *Adenocystis utricularis* and *Iridaea cordata* in the middle intertidal of King George Island from December 1996 to February 1998. Percentage covers with on standard error of canopy-understorey space. Station 1 is situated at M.H.W.N. and station 7 at M.L.W.N..
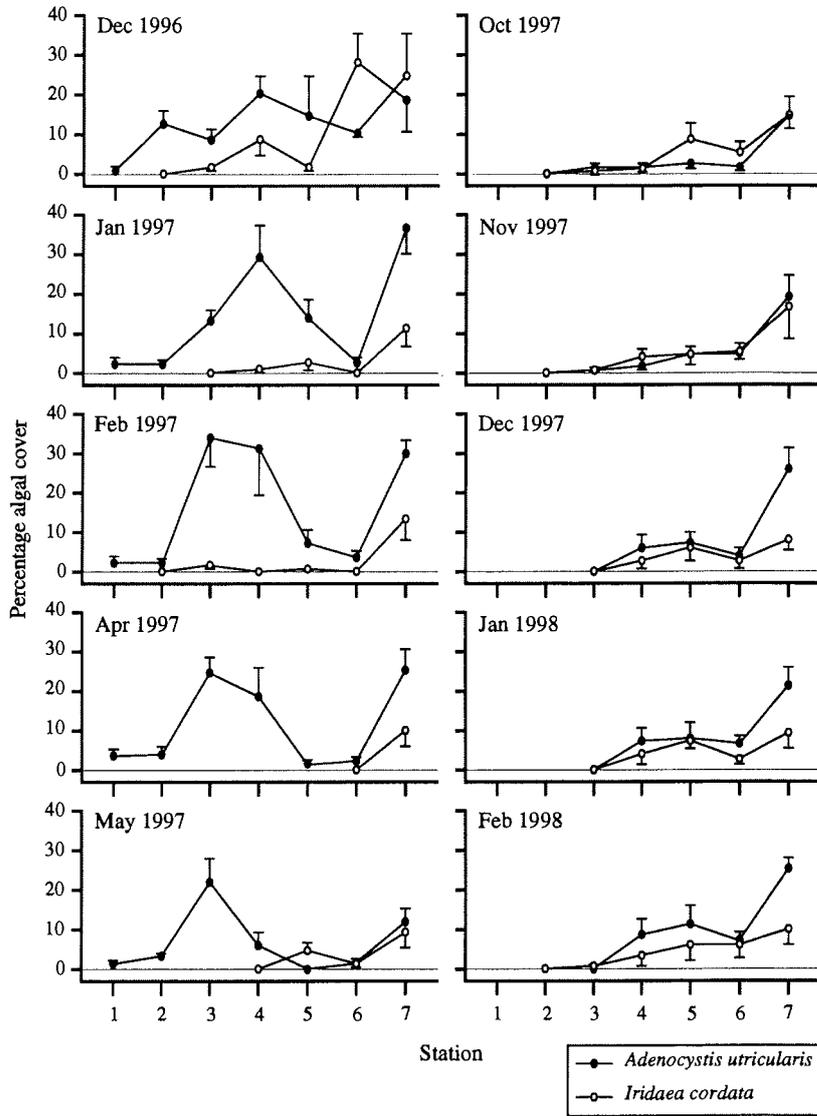
Fig. 3.15. Vertical distribution of *Adenocystis utricularis* and *Iridaea cordata* in the middle intertidal of King George Island from December 1996 to February 1998. Percentage covers with on standard error of canopy-understorey space. Station 1 is situated at M.H.W.N. and station 7 at M.L.W.N..

intertidal during the winter 1997. A significant difference in primary and canopy-understorey space was found during the summer 1996/97. After its abundance significantly decreased from December 1996 to January 1997, it did not change until May 1997. On the other hand, the abundance was approximately constant in the course of the summer 1997/98. Percentage covers of *I. cordata* were positively correlated with tidal levels. This distribution pattern was constant during the whole sampling period.

The data of primary and canopy-understorey space of *Iridaea cordata* were analysed with a three-factor ANOVA (year, month and tidal level) (Table 3.3). There were no significant differences in primary space, except between the tidal levels. Furthermore, there was no significant difference in primary space between the time before the formation and after

Table 3.3. ANOVA of the effect of year, month and tide level on percentage cover (primary space) of *Adenocystis utricularis* and *Iridaea cordata*. Data only from December to February are used. All data were transformed by the angular transformation.

Source of variation	df	Adenocystis utricularis			Iridaea cordata		
		MS	F		MS	F	
Year (first and second summer)	1	6746	111.49	***	33	0.93	ns
Month (from December to February)	2	21	0.34	ns	80	2.30	ns
Year x Month	2	39	0.64	ns	55	1.57	ns
Tide level (TL)	6	1704	28.17	***	645	18.48	***
Year x TL	6	459	7.59	***	50	1.42	ns
Month x Level	12	173	2.87	***	42	1.22	ns
Year x Month x TL	12	204	3.36	***	58	1.66	ns
Residual	252	61			35		

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns is not significant, $P > 0.05$.

receding of ice foot. Thus, *I. cordata* seems to show no seasonality or interannual variation. *I. cordata* inhabited the lower stations and its percentage cover and distribution were relatively constant during whole sampling period (Fig. 3.15).

receding of ice foot. Thus, *I. cordata* seems to show no seasonality or interannual variation. *I. cordata* inhabited the lower stations and its percentage cover and distribution were relatively constant during whole sampling period (Fig. 3.15).

3.3.3. Effect of ice disturbance and grazers on the intertidal algae

Ice disturbance

For the effect of ice foot on intertidal algae, data of primary space of *Adenocystis utricularis* and *Iridaea cordata* were divided in the ice-foot zone (station 1 - 4) and below the ice-foot zone (station 5 - 7), and those were compared again before formation (May 1997) and after receding of the ice foot (October 1997). The primary space of *A. utricularis* significantly changed during the formation of the ice foot (Fig. 3.16 and Table 3.4). A significant interaction between time and zone, however, was found. The primary

a. *Adenocystis utricularis*   b. *Iridaea cordata*
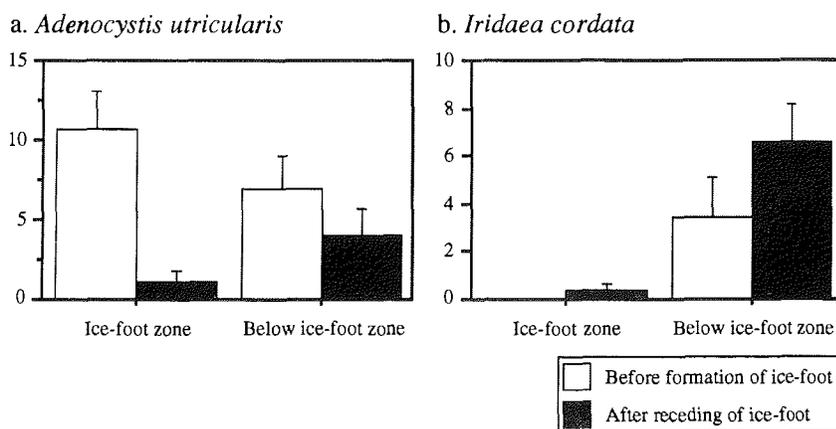
Fig. 3.16. Effect of ice foot on *Adenocystis utricularis* and *Iridaea cordata* in the middle intertidal of King George Island. Percentage covers with standard error of primary space. Ice-foot zone: station 1 - 4; below ice-foot zone: station 5 - 7; before formation of ice foot: May 1997 and after receding of ice foot: October 1997. Station 1 is situated at M.H.W.N. and station 7 at M.L.W.N..

space of *A. utricularis* between station 5 and 7 did not change during the formation of the ice foot whereas the ice foot effectively reduced macroalgae between station 1 and 4. On the other hand, primary space of *I. cordata* did not change significantly during the formation of the ice foot. Between station 1 and 4, most of *I. cordata* disappeared before the formation of the ice foot.

Table 3.4 ANOVA of the effect of the ice foot on primary space of *Adenocystis utricularis* and *Iridaea cordata*. Data are compared before formation (May 1997) vs. receding of ice foot (October 1997) and in the ice-foot zone (station 1 − 4) vs. below the ice foot-zone (station 5 - 7). All data were transformed by the angular transformation.

Source of variation	df	Adenocystis utricularis			Iridaea cordata		
		MS	F		MS	F	
Time (before vs. after ice foot)	1	911.1	13.55	***	68.6	2.89	ns
Zone (below vs. in ice foot zone)	1	4.5	0.07	ns	551.5	23.22	***
Time x Zone	1	265.7	3.95	*	44.7	1.88	ns
Residual	94	67.3					

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns is not significant, $P > 0.05$.

Grazers

Linear regression between density of *Nacella concinna* and macroalgae was used in order to test the effect of grazing on macroalgae. A significant negative relationship between the density of *N. concinna* and the total primary space of algae (except for *A. utricularis* and *I. cordata*) was observed in the first ($r^2 = 0.74$, $F = 78.04$, $P < 0.001$) and the second summer ($r^2 = 0.43$, $F = 27.6$, $P < 0.001$), respectively (Fig. 3.17).
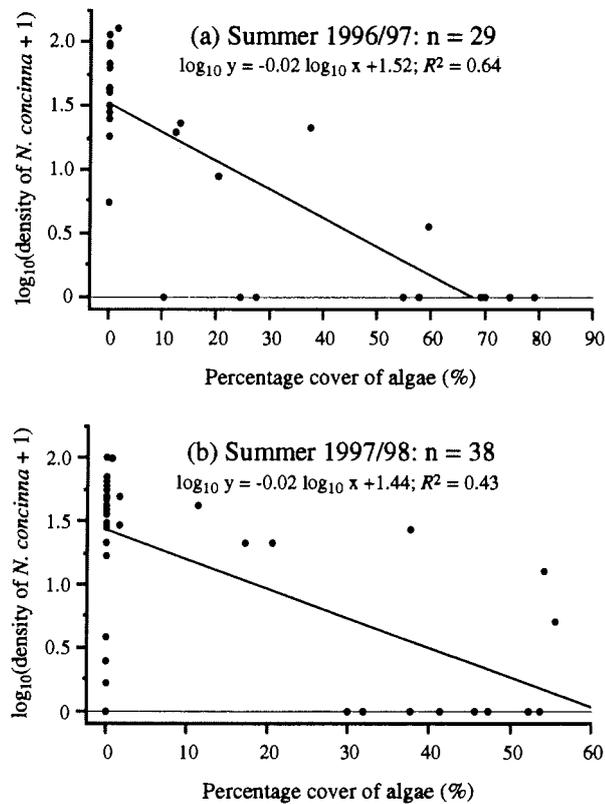
Fig. 3.17. Linear regression between primary space of intertidal algae (except for *Adenocystis utricularis* and *Iridaea cordata*) and density of *Nacella concinna* in the middle intertidal of King George Island in the summer 1996/97 (a: from December 1996 to April 1997) and in the summer 1997/98 (b: from October 1997 to February 1998). Data of percentage cover of primary space were transformed by the angular transformation and data of density of *Nacella concinna* were log-transformed.

3.4. Discussion

In this chapter, I will discuss the temporal and spatial variation of main disturbances affecting intertidal marine algae at first. At the same time, data on intertidal algae will be compared regarding the occurrence of disturbances. Eventually, I will discuss a general pattern in vertical and seasonal distribution of the Antarctic intertidal algae.

3.4.1. Main disturbances affecting intertidal marine algae

In the rocky intertidal of King George Island most species of algae were annual and pseudoperennial except in the lowest intertidal (Fig. 3.2), and their density and distribution showed high seasonality (Table 3.1 and 3.2, and Fig. 3.12 and 3.14). Most macroalgae occurred only in summer, and disappeared from the intertidal before the formation of the ice foot in May, with the exception of *Adenocystis utricularis* and *Iridaea cordata*. The seasonality of macroalgae is primarily connected with the seasonal variability of the light regime in high latitudes (for a review see Wiencke 1996, Clarke 1988). Apart from the light regime, however, biological and physical disturbances can affect density development and distribution of intertidal macroalgae. Major physical disturbances were due to ice and included occurrence of ice foot and floating ice. An important source of biotic disturbance that can affect the abundance of intertidal marine algae is grazing by *Nacella concinna*. In this study those main disturbances showed high temporal and spatial variation (Fig. 3.18).

3.4.1.1. Ice foot

As physical disturbances, the ice foot formed in winter (from July to September 1997), whereas ice scouring caused by floating ice occurred in summer (Fig. 3.18 a). The duration and stretch of the ice foot depends on meteorological conditions, currents and substratum

40

profiles (Walker 1972). As observed in this study, on a steep shore the ice foot extends further down than on a less steep shore (Fig. 3.18 b). On a steep shore, sea water froze during low-water of the spring tides and covered the rock surface. On a less steep shore, pancake ice was beached and covered by snow, forming a network of ice tunnels between pancake ice in the lower intertidal. The ice tunnels, which were connected to the sub-tidal, protected the mid-intertidal zone in winter. Those protected ice tunnels were also observed at Signy Island (Walker 1972) and in Arthur Harbour (Shabica 1972). In spite of a marked reduction in size and number of individuals, *Iridaea cordata* (Shabica 1972) and *Adenocystis utricularis* were observed in the lower intertidal (lower than station 5) under fast ice during the winter of 1997, although markedly reduced in size and number of individuals.

The ice foot encases the rock surface and can freeze inhabiting biota (Ellis and Wilce 1961, Stephenson and Stephenson 1972). As the ice thaws, plants may be ripped off the substratum (Mathieson et al. 1982). As the ice foot broke out at the end of October 1997, bare rock was observed at station 1 and 2 only. In addition, a significant reduction of the abundance of *Adenocystis utricularis* between station 1 and 4 from May to October (Table 3.4 and Fig. 3.17) suggests that ice foot is, among others, one important factor for upper limit restriction of this species. Except for *A. utricularis*, *Iridaea cordata* and *Porphyra endiviifolium*, however, most intertidal algae disappeared from the intertidal before the formation of an ice foot. The ice foot probably was not responsible for disappearance of most algae in autumn (Fig. 3.12).

The ice foot was only present in the upper intertidal during the winter of 1996, which was recorded as a warm year (mean temperature was about 1.3 C° higher than the mean of the last eight years from 1988 to 1995, Kang et al. 1997 and personal communication with overwintering members), whereas it formed from May to October in 1997. The knowledge of life histories of some Antarctic macroalgae has been recently increased through successful isolation and cultivation (Wiencke 1996). Because algal spores lack a dormancy period, the macroalgae may be able to survive the harsh winter conditions as microscopic forms (germlings, microtalli or filaments) (a "bank" of microscopic forms, Santelices

1990, Santelices et al. 1995). Thus, the availability of a local "bank" in a certain area is probably important in the development of macroalgae in spring. No information about the effect of ice foot on the "bank" is available. However, if "banks" of microscopic forms are

a. Temporal variation of disturbances

b. Spatial variation of disturbances
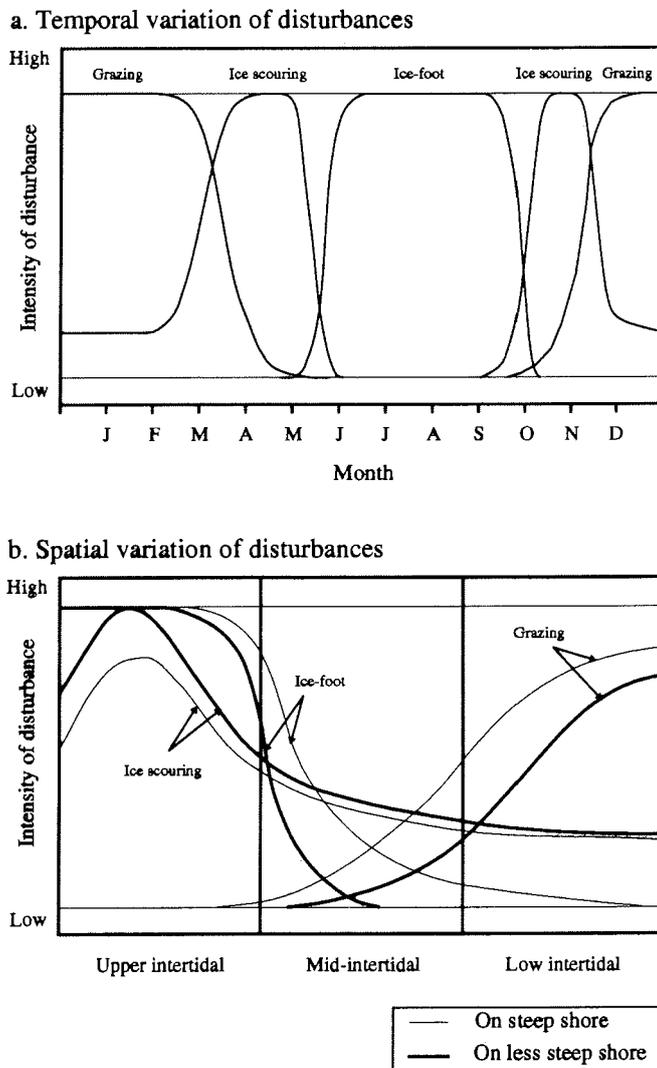
Fig. 3.18. Temporal (a) and spatial (b) variation of main disturbance (ice foot, ice scouring and grazing by *Nacella concinna*) in the intertidal of King George Island.

effectively disturbed by an ice foot in winter, the interannual variation of algal distribution

in the middle intertidal would be linked in part to the formation of an ice foot. More studies

on the influence of an ice foot on "banks" of microscopic forms in winter are needed.

3.4.1.2. Ice scour

Ice scour is caused by floating ice grounding and scraping on the substratum. It can

effectively denude the substratum of plants and animals in the intertidal (e.g., McCook and

Chapman 1991, Minchinton et al. 1997, Pugh and Davenport 1997). Floating ice originates

from ice pieces breaking away either from glaciers, icebergs, or sea ice (Dinsmore 1972).

The extent of damage to intertidal assemblages from scouring by floating ice is highly

variable (Fig. 3.18). This study shows clearly seasonal variation of ice scouring. The

sampling area in Barton Peninsula is located far away from glaciers both in Potter and

Marian Cove, so that ice pieces from the glaciers might occur less frequently than in those

coves. Pancake ice and ice pieces that broke from sea ice severely disturbed the study area,

but only just before formation and after breaking of sea ice, whereas disturbance was less

intense from December to February (Fig. 3.8). Thus there was an opportunity for some

ephemeral algae to colonise our sampling area in summer. On the other hand, the reduction

of macroalgae in autumn could be partly connected to the disturbance by floating ice.

Apart from seasonal variation, disturbance by ice scouring can show a spatial variation

(Fig. 3.18 b). The upper intertidal, at least on the flat shore where large numbers of small

floating ice pieces were beached, was significantly more disturbed by the floating ice than

the lower intertidal. It is likely that the residence time of disturbance by scouring of

floating ice is much longer on the flat shore than on the vertical rock. Most macroalgae

scarcely occurred at station 1 and 2, with exception of filamentous algae which rapidly

spread and *Porphyra endiviifolium* and *Acrosiphonia arcta*, which colonised in January

and February.

3.4.1.3. Grazing

In contrast to shores in other parts of the world, where grazers occur all year round in spite of variability of abundance (e.g., May et al. 1970, Underwood 1981, Cubit 1984, Underwood and Jernakoff 1984), *Nacella concinna* migrates seasonally in the Antarctic intertidal (Fig. 3.10 and Fig. 3.18). The importance of algal-herbivore interactions influencing the structure of marine communities is well known (see reviews by Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Hawkins and Hartnoll 1983). The limpet *N. concinna* is a herbivore, grazing on microphytobenthos (Shabica 1976, Brand 1980, Iken 1995, Brêthes et al. 1994), calcareous rhodophytes (Brand 1980) and seaweed (Iken 1995). Some evidence that the limpets selectively graze on filamentous, or membranous algae and benthic diatoms has been documented (Castenholz 1961, Nicotri 1977, Cubit 1984, Farrell 1988, Kim 1997). A negative correlation between the density of limpets and percentage cover of diatom film and filamentous algae (Fig. 3.16) indicates effective grazing of limpets on those species. We found that the distribution of filamentous algae in the first summer was restricted to the upper parts of the sampling area. However, filamentous algae were able to grow in the lower intertidal (unpublished data by removal experiment of limpets at station 6). Furthermore, their lower limits moved upwards and coincided with the upper limits of the distribution of limpets, although the percentage cover of filamentous algae increased in the upper part of the sampling area until February 1997. Therefore, discrepancies in determination of the lower limits of filamentous algae (e.g., Delépine and Hureau 1963, Hedgpeth 1971, Ramirez and Villouta 1984, Castilla and Rozbazylo 1985) could be related to seasonal migration and grazing of limpets.

Since most intertidal macroalgae were ephemeral and appeared in spring and limpets have been known as effective grazers on macroalgal propagules (Underwood 1981, Jernakoff 1983, 1985, see also Santelices 1990), migration of *Nacella concinna* in spring may have been important for the later distribution of macroalgae. The poor development of *Monostroma hariotii* and *Palmaria decipiens* between station 5 and 7, and of *Adenocystis utricularis* and *Iridaea cordata* at station 6 and 7 during the first summer (Fig. 3.13 and

3.15) could at least partially be explained by grazing on their propagules in spring. However, when macroalgae were well developed in summer, grazing by *N. concinna* on those algae seemed to be less severe. This finding should, however, be verified by enclosure experiments. In fact, there was no significant difference in the density of *A. utricularis* and *I. cordata* from December to May. Although the density of *M. hariotii* and *P. decipiens* were reduced during these periods, neither their distribution nor their lower limits changed. It is more likely that strong wave action and ice scouring that occasionally occurred during summer destroyed those species that grew over 20 cm in length at the end of December.

A comparison of the vertical distribution of *Nacella concinna* between the two summers indicates that there is interannual variation of upward migration. Another possibility is that the upward migration could be delayed by high densities of macroalgae. Comparing the vertical distribution in December of the two summers, upper limits of limpets extended to station 2 in the second summer, while they reached station 5 only in the first summer. It is likely that dense macroalgal cover (e.g., 55.6 % of primary space in zone 4 in December 1996) was an obstacle that effectively prevented the further upward migration of limpets. Furthermore, limpets move further when food availability is low (Cubit 1984), so it is possible that there was no need to travel so far to obtain their quota of food in the first summer. Thus, the disturbance by grazing limpets seems to be an event that varies spatially and temporally.

3.4.2. General patterns of vertical distribution

Although there was a high seasonality and large interannual variation, a rough zonation of macroalgae was nevertheless recognisable. The results of this study are very similar to earlier descriptions of the shores of King George Island (Zielinski 1990, Petrov and Nikolaev 1984) and coincide with the observation of three intertidal fringes in Robert Island (Castilla and Rozbaczylo 1985). The upper intertidal is characterised by *Porphyra*

endiviifolium and *Urospora penicilliformis*, the middle by *Adenocystis utricularis* and *Iridaea cordata* and the lower intertidal fringe by lithothamnioid and some sublittoral macroalgae.

In general, in the supralittoral zone being free of ice and snow *Prasiola crispa* occurs during the Antarctic summer (Delépine 1966, Zielinski 1990). On shores of the upper intertidal, there were no grazers such as *Nacella concinna* and *Naevilittorina* sp. On the other hand, the entire zone was heavily disturbed by ice foot in winter for about four months in Maxwell Bay, but ice influence on the upper intertidal seems to have been rather constant with substrate profile and heterogeneity. One of the important disturbances that showed seasonal and spatial variation was ice scour caused by floating ice. The occurrence of *Porphyra endiviifolium* with filamentous algae in the upper intertidal and *Enteromorpha* sp. in the splash pools and crevices during summer coincide with many earlier observations (Hedgpeth 1971, Petrov and Nikolaev 1984, Ramirez and Villouta 1984, Castilla and Rozbaczylo 1985, Stockton 1990, Zielinski 1990). Those may have grown only on the exposed steep rocky shore where they were confined to relatively protected cracks, while most of the upper intertidal was barren because of ice scouring.

The middle intertidal zone was heavily disturbed by ice foot during winter and floating ice during summer and those disturbances were temporally and spatially variable in this zone. The important grazer *N. concinna* migrated seasonally up to the middle shore. Beside *Nacella concinna*, at least two species of *Naevilittorina* inhabited this region which were very abundant in the crevices. Consequently, the density, assemblages and vertical distribution of macroalgae in this zone showed high seasonality and large variation. In general, *Iridaea cordata* and *Adenocystis utricularis* grow scattered in the middle intertidal fringe. Their upper limits change from year to year, and are probably linked with the extension of ice foot in winter. The belt of filamentous algae in the upper intertidal extended to the upper part of this zone, and their density and lower limits of distribution seemed to be changed due to grazing of *N. concinna*. The ephemeral alga *M. hariotii* and the red alga *P. decipiens* can rapidly spread into the middle intertidal during summer. We observed these species only on flat shores in the first summer. Consequently, their

occurrence and distribution in the middle intertidal seems to be confined by the extension of ice foot and grazing by limpets on propagules in spring.

The lower intertidal fringe seems to be less disturbed by ice foot and ice scouring, at least in Maxwell Bay. However, limpets grazed throughout the year. In general, infralittoral fringe and lower tide pools were characterised by patchiness of perennial macroalgae, with few sessile animals (*Silicularia rosea*, *Kidderia* sp. and *Lasaea* sp.) and abundant grazers (*Laevilittorina* sp., *Nacella concinna* and some other gastropods). Most macroalgae were found all year round in sheltered areas and rock crevices where the floating ice is not able to cause damage, although their macrothalli reduced in winter. Macrothalli of some species of algae, such as the annual *Phaeurus antarcticus*, completely disappeared in winter. Lithothamnioid algae inhabited the majority of the tide pools. Ephemeral algae such as *M. hariotii* and *P. decipiens* were found in summer only, but less abundant. The presence of *N. concinna* all year round at low levels on the shore might be associated with the poor development of some ephemeral algae.

In summary, in the Antarctic rocky intertidal most species of algae are annual and pseudo-perennial, and their density and distribution show high seasonality and large year to year variation. Seasonality and variation are primarily connected with seasonal variability of the light regime in high latitudes. Furthermore, disturbance by the ice foot, ice scouring and grazing vary spatially and temporally. Duration and extension of the ice foot may affect the spatial and temporal variation of vertical distribution of macroalgae in the middle intertidal. The abundance and spatial variation of macroalgae can be affected by ice scouring. *N. concinna* migrates seasonally from the sublittoral to the intertidal in summer and back in winter. Upward migration can be delayed by high densities of macroalgae. Density of filamentous algae and propagules of macroalgae may be regulated by grazing of *N. concinna*. Therefore, timing, intensity and duration of disturbance are important, especially for the initial colonisation of macroalgae, which might influence their later density and distribution.

Chapter 4

Population structure of *Nacella concinna*

4.1. Introduction

Many intertidal limpets undergo vertical migration, which allow animals to regulate their spatial and temporal distribution to some extent and which sometimes manifests as intraspecific size differences at different tidal levels (Frank 1965, Haven 1971, Breen 1972, Branch 1975 a, Hobday 1995). Several factors are considered to affect the migratory habits of limpets, such as avoidance of response to competition (Frank 1965, Branch 1975 a), environmental changes (Lewis 1954, Frank 1965), predators (Phillips 1975, 1976) and food availability (Branch 1975 a, Cubit 1984).

According to Walker (1972) the population of *Nacella concinna* at Signy Island consists of two sub-groups. One group migrates to the intertidal in spring and summer, and back to the sublittoral in autumn. The other group remains in the sublittoral all year. The two groups can be distinguished by their shell morphology. The summer intertidal limpets have a larger height/length ratio and the shells lack epibiota (Walker 1972, Nolan 1991). Since the two sub-groups are genetically identical (Beaumont and Wei 1991), it has been suggested that environmentally induced, phenotypic changes are responsible for the differences between the two shell forms (Walker 1972, Nolan 1991).

The kelp gull *Larus dominicanus* is known to be an important predator of intertidal *Nacella concinna* (Hedgpeth 1971, Shabica 1976, Fraser 1989, Favero et al. 1997, Favero and Silva 1998, Cadée 1999, Silva et al. 1999). Information from both the Antarctic and sub-Antarctic indicates that kelp gulls select large limpet sizes (Branch 1985, Fraser 1989, Cadée 1999, Silva et al. 1999) and can modify the population structure. Previous data on consumption rates indicate that kelp gulls eliminate 10 – 14 % of *N. concinna* per year in the intertidal of King George Island (Silva et al. 1999) and about 20 % of *N. delesserti* per year at sub-Antarctic Marion Island (Blankley and Grindley 1985, Branch 1985). The gull

feeds predominantly in shallow water during spring low tide (Favero et al. 1997, Cadée 1999). After the kelp gulls have ingested *N. concinna*, the shells are dropped as regurgitates. Shells too large to ingest are cleaned first, and then the flesh is consumed on higher places in the intertidal zone (Shabica 1971, Favero et al. 1997, Cadée 1999).

This chapter concentrates on population structure of *Nacella concinna* and possible factors that can control it. First, I will describe seasonal patterns in the population structure and some differences between the intertidal and sublittoral population. In a next step, I also investigated the behavioural patterns that could maintain the population structure. In addition, I checked whether the kelp gulls select limpets of particular sizes.

4.2. Material and methods

Population structure

To sample *Nacella concinna*, the same stations and quadrats that were described in the Chapter 3.2 were used. From December 1996 to October 1997 and March 1998, limpets were collected on quadrats (3 to 8) until the number of limpets exceeded at least thirty at a station. From November 1997 to February 1998, all individuals were collected within 8 quadrats at a station. During the winter, an additional sampling was conducted in a tidal pool near the transect. Furthermore, sublittoral limpets were collected from depths of 15 m and 20 m by SCUBA diving in February 1998. After the sex of each individual was determined, shell length, height and width were measured to ± 0.01 mm with Vernier Callipers.

For statistical analysis, data of station 8 were excluded because the sampling could not be performed every month. The correlation between the limpet size (shell length, mm) and tidal level (distance from station 7, m) was checked with a regression analysis. A two-way ANCOVA was used to determine if the regression of shell length on tidal level differed among months and sexes. For the relationship between shell height (y) and shell length (x), data of individuals larger than 20 mm were used and a simple linear regression was used. This lower shell length limit was chosen following the observations of Walker (1972) of a change in the shell length/height relationship being evident only in those animals over 20 mm in length. To compare the relationships among the different habitats (intertidal and sublittoral) or sexes, a one-way ANCOVA was used.

Migratory behaviour

To determine the migratory pattern of *Nacella concinna*, mark-recapture experiments were conducted from March 1997 to February 1998. For the seasonal pattern in migratory behaviour, one fixed zone (zone 1) with an area of 30 m² (6 m in the horizontal direction x 5 m in the vertical direction) was established at M.L.W.S. in March 1997. The experiments were separatety performed in autumn, spring and summer. In order to compare the

migratory behaviour between the different tidal levels, one additional zone (zone 2) with the same area as zone 1 was established at M.H.W.S. (the upper limits of limpets in summer) in November 1997.

In order to test the hypothesis that individual migration could maintain the pattern of size gradient on shore, the collected limpets were divided into two size classes; shell length between 23 and 25 mm, and shell length between 30 and 32 mm. All experimental limpets were collected from a tidal pool near the experimental area, since small limpets were not present in the intertidal at some seasons. In addition, to compare the migratory behaviour between the intertidal and sublittoral limpets, the sublittoral limpets of a shell size between 30 and 32 mm were collected at 15 m depth and released in the intertidal in March 1997. All limpets were marked with a lettered plastic tag (5 x 5 mm) attached to the shell with epoxy resin. About 40 large and 40 small limpets were replaced in each experimental zone. The animals were released immediately after marking and sprayed with seawater for 10 minutes to assist reattachment. This procedure allowed the subsequent positions to be recorded without disturbing the animals. The position of each animal was recorded, for the first time, at least 24 h after release.

The positions of marked limpets were recorded using the method described by Underwood (1977). The distance from the centre of the shell to two nails driven into the rock in a distance of 1751 cm specified the position of each limpet. The distance and direction moved by a limpet over a period of time were calculated by coordinate geometry (upward movement: positive). The up/down axis was perpendicular to the shoreline. 90° was defined as straight up the beach (positive value); 270° was straight down (negative value). All measurements were performed during the ebb of the spring tides. After about 15 days from the initial record, the limpets marked were searched for and their distances to the two nails were measured. During this time frame both neap and spring tides occurred.

The directions and distances moved were analysed with a modified Rayleigh´s test (Moore 1980). Because the periods from releasing to recapturing the limpets were different, all data were represented by distances moved per day (speed: distances moved within an experimental period / experimental days). For the statistic, the vertical distances moved

were used, ignoring lateral movements because the Rayleigh´s test indicated that limpets moved, in most cases, vertically. Since the variances of distances moved were unequal after logarithmic transformation, non-parametric methods of analysis were employed for the statistical test. To test the difference in the distances moved among the different seasons, Kruskal-Wallis test was used. The differences among two zones, two sizes, or between the intertidal and sublittoral limpets were tested by the Mann-Whitney U test.

Predation of Larus dominicanus

In order to determine the seasonal predatory press of kelp gull *Larus dominicanus* on *Nacella concinna*, the regurgitated pellets by the kelp gulls were studied from June to November 1997. The pellets were collected in a 1.2 km stretch along the shore (Fig. 2.1 B). At the beginning of June, all the deposited limpet shells in gull feeding piles were removed along the coast in about 10-m from M.H.W.S. (mean high water of spring tides). In this period, the whole of the beach was covered with snow, so that the freshly produced limpet shells could be easily found. Four weeks later a first collection was made of all newly deposited shells without separating pellets. After that the deposited limpet shells were collected once a week, separately in each pellet. In addition, to determine the size selectivity by kelp gulls on limpets, all living limpets were collected in shallow tidal pools, where the feeding by gulls was frequently observed, at the end of October.

Fragments with apex only were counted from the collected limpet shells. Length, width, and height of the intact shells were measured to the nearest 0.1 mm, using a Vernier Calliper. In comparison to the height, the width of limpet shells was more significantly correlated with the length. In cases where the shells had been crushed, therefore, shell width was measured and shell length calculated from a regression of shell length (Y: mm) on shell thickness (X: mm):

$$Y = 2.345 + 1.31 \, X \quad (r^2 = 0.96, P < 0.0001)$$

4.3. Results

4.3.1. Size distribution

The size structure of the population was studied through the analysis of size frequency distribution and the regression analysis of shell length on tidal level. A total of 3,744 individuals was obtained in the collections of the intertidal transect and the shell sizes ranging from 8 to 43.1 mm. Mean size of *Nacella concinna* was 28.96 mm (± 0.06 SE) and significantly varied with months (Table 4.1). Length-frequency distributions, however, were unimodal and homogeneous in each month (Fig. 4.1). Most individuals of the intertidal population (99.6 %, data from Station 1 to 7 only) were larger than 20 mm shell length.

The length-frequency distributions by tidal level were broadly overlapping, but showed increasing means at successively higher tidal levels. Thus, the shell size of *N. concinna* increased significantly with tidal level (Fig. 4.2 and Table 4.2). However, covariance analysis indicated that the shell size gradients of *N. concinna* on tidal level varied with month (Table 4.1). The slopes of regression were steeper at the beginning of the upward migration.

Table 4.1. Full interaction of ANCOVA for the shell length (mm) vs tidal level (distance from station 8, meter) with covariates time (month) and sex. Time is fixed and level on shore is variable. Data only from station 1 to 7 are used (excluding data of April 1997).

Source of variation	df	MS	F
Time (Month, T)	10	70.20	7.05***
Level on shore (meter, H)	1	1058.06	106.30***
T x H	10	52.91	5.32***
Residual	2940	9.95	

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns is not significant, $P > 0.05$
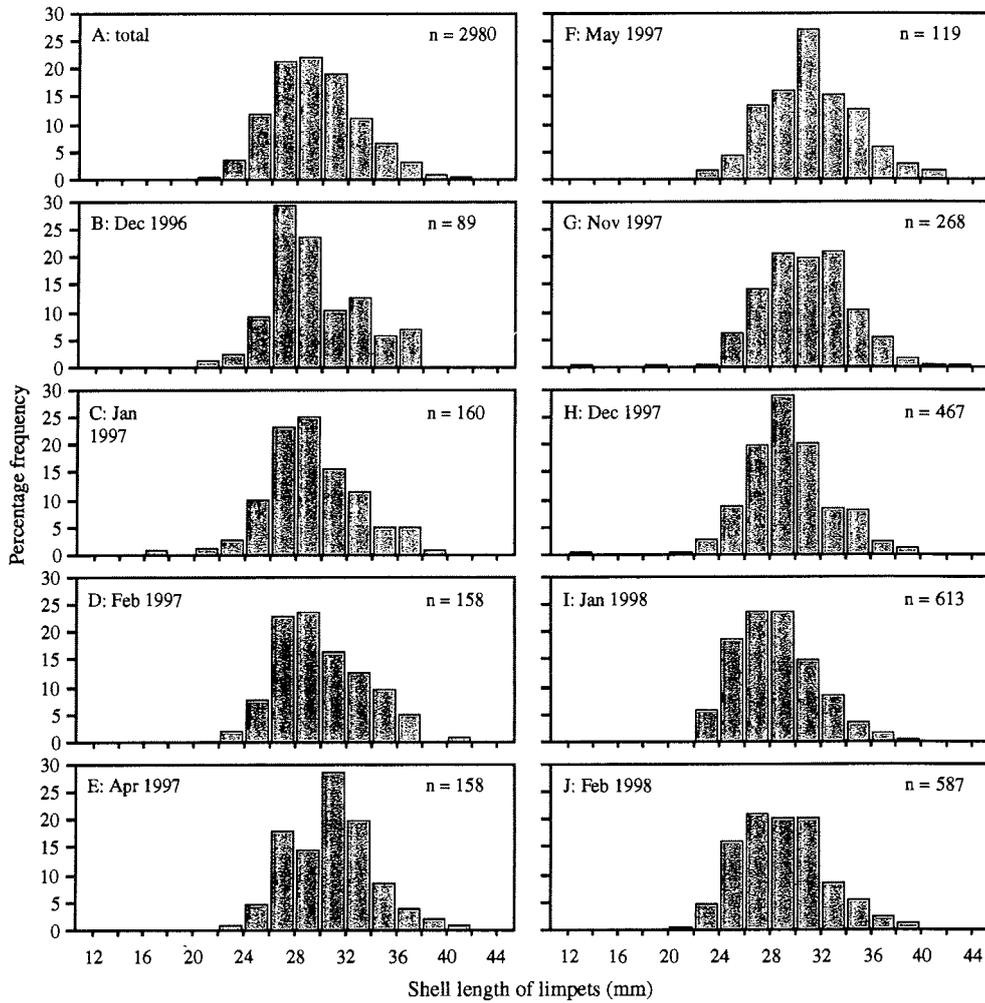
Fig. 4.1. Frequency histogram of *Nacella concinna* in the intertidal. Pooled data from Station 1 to 7 (in April from Station 1 to 6 only).
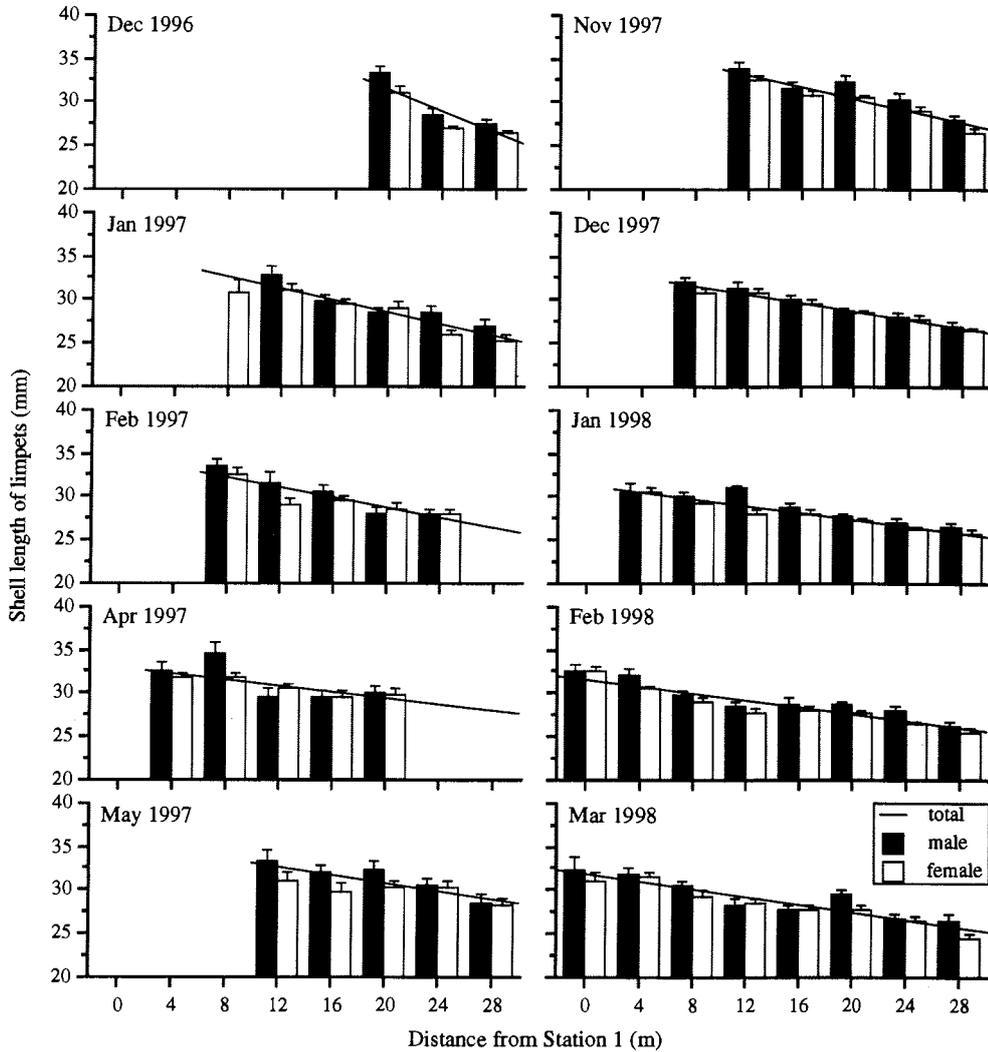
Fig. 4.2. Linear regressions (line) of shell length of *Nacella concinna* (mm) vs distance from Station 1 (m). Vertical bars represent mean shell sizes of males and females with one standard error.

Mean shell size of male limpets (29.33 ± 0.099 SE mm, n = 1405) was significantly larger than the one of females (28.82 ± 0.08 SE mm, n = 1911) (Fig. 4.2 and Table 4.3). Since there was no significant interaction in terms of the sex (Table 4.2), the mean shell length of

the males was, in most cases, larger at each tidal level than that of the females (Fig. 4.2). On the other hand, there was no significant difference in mean shell size between male and female limpets in the sublittoral population $(t_{1,209} = 0.202, P > 0.05)$.

Table 4.2. Regression equation of shell length (Y, mm) of *Nacella concinna* on tidal level (X, distance from station 8, m).

Month	n	Regression equation	r^2	F
December 1996	196	Y = 26.44 + 0.60 X	0.211	51.85***
January 1997	202	Y = 25.94 + 0.33 X	0.268	73.06***
February 1997	158	Y = 26.41 + 0.30 X	0.231	46.95***
April 1997	158	Y = 27.95 + 0.18 X	0.097	15.77***
May 1997	149	Y = 29.15 + 0.20 X	0.092	14.82***
August 1997	57	Y = 26.48 + 0.57 X	0.094	5.71*
October 1997	64	Y = 30.64 + 0.05 X	0.001	0.05ns
November 1997	338	Y = 27.60 + 0.35 X	0.237	104.15***
December 1997	581	Y = 26.78 + 0.25 X	0.218	161.33***
January 1997	737	Y = 25.94 + 0.20 X	0.162	143.28***
February 1997	690	Y = 26.17 + 0.19 X	0.233	209.08***
March 1997	414	Y = 25.81 + 0.22 X	0.262	146.61***

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns is not significant, $P > 0.05$

Table 4.3. Full interaction of ANCOVA for the shell length (mm) vs tidal level (distance from station 8, meter) with covariates time (month) and sex. Time and sex are fixed, and level on shore is variable. Data only from station 1 to 7 are used (excluding data of April 1997). Interaction of time x level on shore x sex is not significant $(P > 0.25)$ and hence not shown in the table.

Source of variation	df	MS	F
Time (Month, T)	10	75.96	7.99***
Level on shore (H)	1	996.33	104.77***
Sex (S)	1	149.80	15.75***
T x H	10	47.88	5.03***
T x S	10	14.64	1.54ns
H x S	1	2.52	0.27ns
Residual	2926	9.51	

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns is not significant, $P > 0.05$

5.3.5. Sex ratio

In *Nacella concinna* the sexes are separate. The sex ratio of intertidal limpets was 1:1.359

(male:female, n = 3316), which is significantly different from 1:1 (χ^2 = 7.39, P < 0.001). In
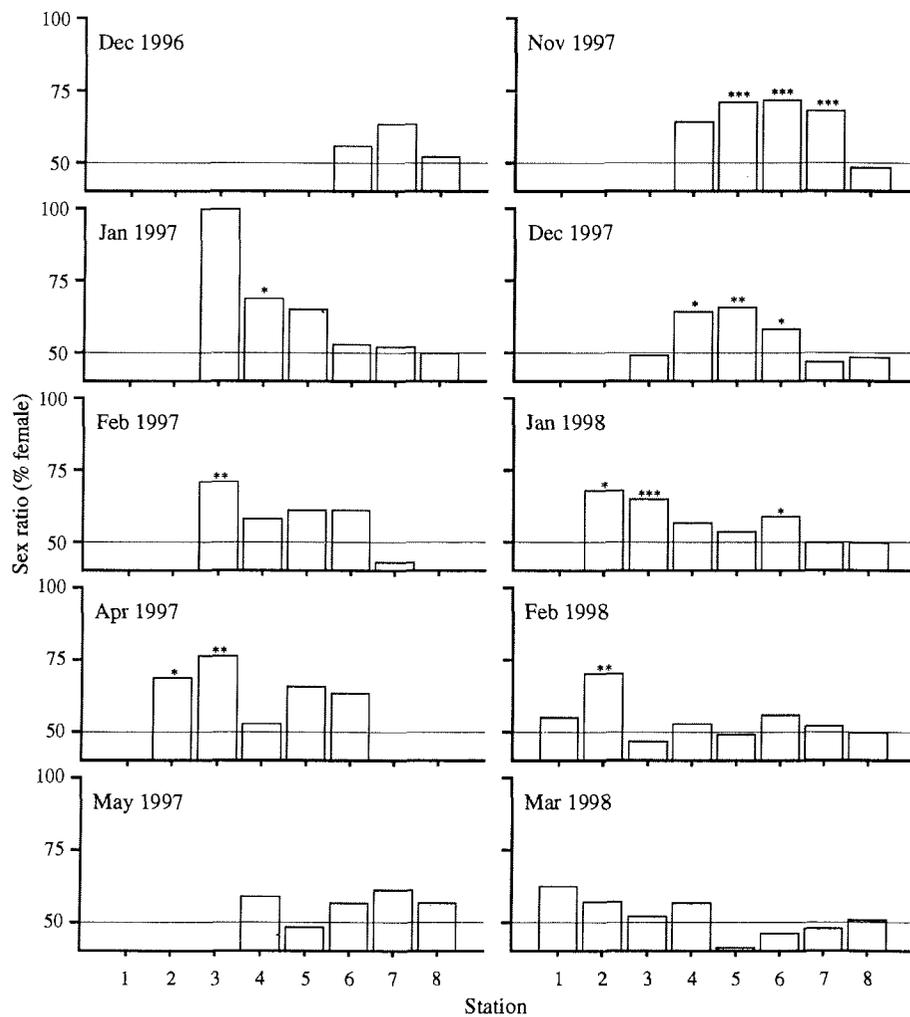
Fig. 4.3. Vertical distribution of sex ratio (% females) in *Nacella concinna*. * denotes significant P < 0.05; ** P < 0.01; *** P < 0.001; ns is not significant, P > 0.05 difference from 50 % by (χ^2-test).

contrast to the intertidal limpets, the sex ratio of sublittoral limpets was 1:0.981 (male:female, n = 211; χ^2 = 0.015, P > 0.05). Females usually outnumbered males in the upper part of the intertidal, particularly at the beginning of migration. In contrast, the sex ratios were approximately 1:1 in the lower intertidal (Fig. 4.3).

Fig. 4.4 shows the sex ratio in each shell size class. For the intertidal limpets a definite bias exists with a significant tendency for the young population (between 20 and 30 mm shell length) to be female. The maximum proportion of females was recorded in the limpets between 22 and 24 mm long. Beyond this point, the proportion of females decreased constantly and the limpets larger than 32 mm exhibited a bias to be male. On the other hand, the sex ratio of the sublittoral limpets did not differ from 50 % in all size classes.
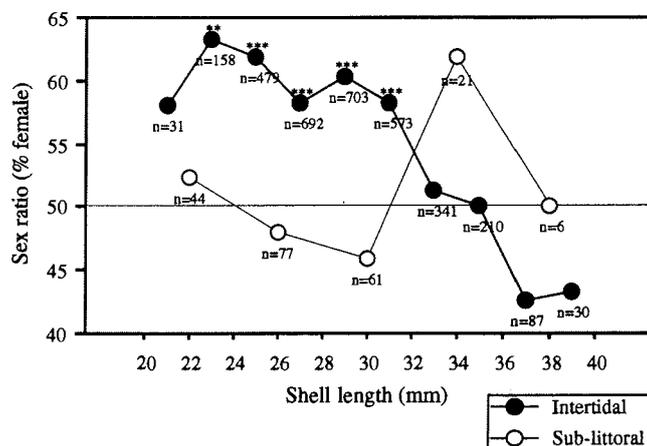
Fig. 4.4. Sex ratio (% female) for 1 mm categories of adults of *Nacella concinna*. * denotes significant P < 0.05; ** P < 0.01; *** P < 0.001; ns is not significant, P > 0.05 difference from 50 % by (χ^2-test).

4.3.2. Shell morphology

The relationships between shell length and shell height (larger limpets than 20 mm shell length) are shown in Table 4.4 and Fig. 4.5. In neither the intertidal nor the sublittoral population, the relationships for males and females were significantly different ($P > 0.05$ for slope and intercept). Therefore, in each case, relationships have been calculated for

Table 4.4. Least square regressions of shell length (mm) on shell height (mm). Only limpets larger than 20 mm were used for analysis. x = shell length, y = shell height, n = number of individuals, r^2 = coefficient of determination, F = variance ratio (all $p < 0.001$).

	Regression equation	n	r^2	F
Intertidal				
Males	Y = -6.013 + 0.546 X	1634	0.811	6995
Females	Y = -5.629 + 0.531 X	2181	0.801	8773
Total	Y = -5.812 + 0.538 X	3815	0.806	15862
Sublittoral				
Males	Y = -0.284 + 0.298 X	105	0.648	189
Females	Y = +0.612 + 0.260 X	103	0.634	175
Total	Y = +0.193 + 0.278 X	208	0.636	360
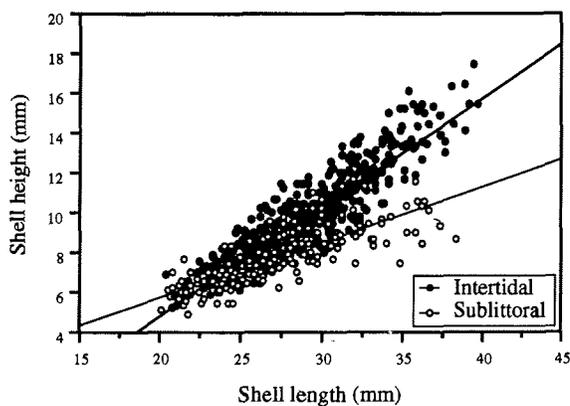
Fig. 4.5. The relationship between shell length (mm) and shell height (mm) in the intertidal and sublittoral populations of *Nacella concinna* in February 1998. Data for individuals larger than 20 mm are used.

both sexes combined. The slopes and intercepts of the relationships differ significantly between the intertidal and sublittoral limpets ($P < 0.001$). Thus, for an animal 30 mm in length, an intertidal individual will have an average height of 10.33 mm, in contrast to 8.36 mm in a sublittoral individual. On the other hand, the relationship of intertidal population differs neither with time nor with tidal level ($P > 0.05$ for both slopes and intercept). Therefore, a clear distinction between the intertidal and sublittoral populations could be recognised and the shell morphology within the intertidal population was uniform.

4.3.4. Migratory behaviour

The Rayleigh´s test indicates that *Nacella concinna* moved, in most cases, vertically up and down in the intertidal, whereas lateral movements were small compared to the vertical ones (Table 4.5). The experiments of the lower intertidal (zone 2) showed a seasonal pattern of the migratory behaviour. In autumn, both large and small limpets exhibited a

Table 4.5. Results of Rayleigh´s test on movement of *Nacella concinna*.

(a) Autumn: zone 2

| | | Intertidal | | | | | | Sublittoral | | |
| | | Large limpets | | | Small limpets | | | Large limpets | | |
	D	n	d	P	n	d	P	n	d	P
26. 03. – 06. 04. 1997	11	18	3	***	19	3	***	18	3	***

(b) Spring and summer

| | | Zone 1 | | | | | | Zone2 | | | | | |
| | | Large limpets | | | Small limpets | | | Large limpets | | | Small limpets | | |
	D	n	d	P	n	d	P	n	d	P	n	d	P
29. 11. – 12. 12. 1997	13	22	0	ns	21	3	***	19	1	**	23	0	ns
16. 01. – 28. 01. 1998	15	24	0	ns	23	3	***	29	0	ns	22	0	ns

D: duration of experiment in days

n: number of recaptured individuals

d: directions moved (1: 315° – 45°, 2: 45° – 135°, 3: 135° – 225° and 4: 225° – 315°; 90° represents a landward perpendicular to the shore)

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns is not significant, $P > 0.05$
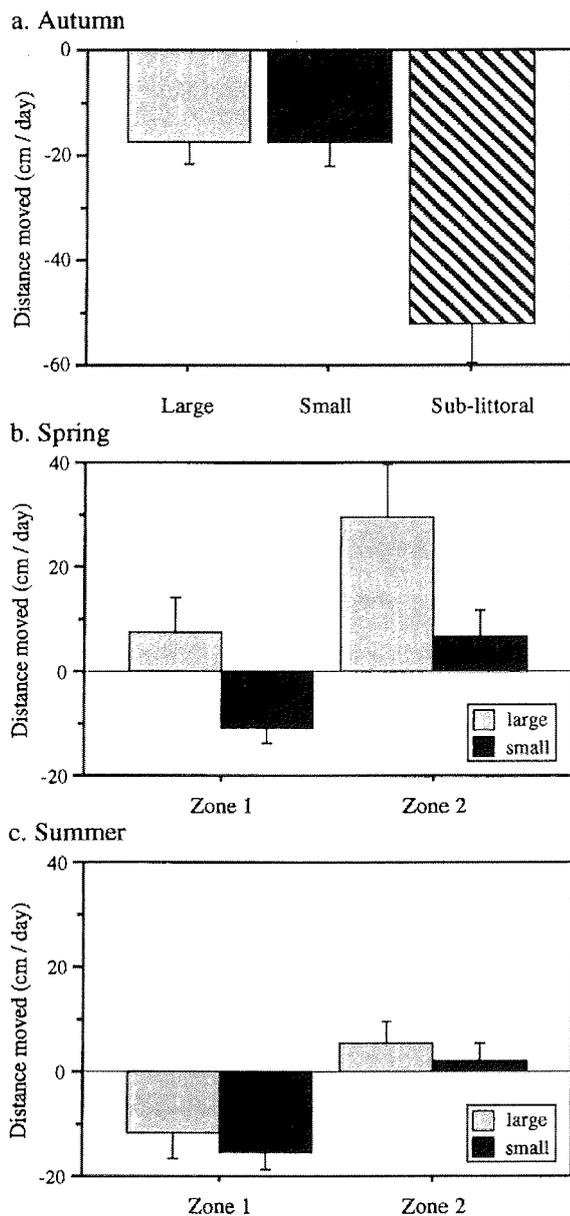
Fig. 4.6. Mean vertical distance moved of marked *Nacella concinna* per day. Vertical bars represent one SE. Large limpets (23 – 25 mm) and small limpets (30 – 32 mm) of the intertidal population, and sublittoral limpets (30 – 32 mm) were compared. The experiment was conducted in M.H.W.S. (zone 1) and M.L.W.S. (zone 2).

significantly downward movement (Table 4.5a and Fig. 4.6a). In spring, large and small limpets moved upwards (Fig. 4.6b), but a significant directional movement was found only for large animals (Table 4.5b). In summer, all limpets moved more or less at random (Table 4.5b and Fig. 4.6c). In the upper intertidal (zone 1), large limpets moved at random during the spring and summer, whereas small limpets showed a significant downward movement (Table 4.5b).

A significant difference in the distance moved a day was found between the intertidal and sublittoral limpets (Mann-Whitney U-test, $P < 0.001$). The sublittoral limpets moved more rapidly downwards with a mean speed of 50 cm a day, in comparison to intertidal limpets with a mean speed of 17 cm a day. When the distances moved a day were compared between large and small limpets, significant differences were found only for the experiment in the spring (Mann-Whitney U-test, all $P < 0.05$). In response to this migratory behaviour, the slopes of the size gradients on tidal level were steeper at the beginning of the upward migration (Chapter 4.3.1).

4.3.5. Predation by kelp gull on *Nacella concinna*

In order to examine whether *Larus dominicanus* selected the limpet size, the mean shell sizes of limpets from pellets and a shallow tidal pool were compared and a significant difference was found (ANOVA, $P < 0.001$). Fig. 4.7 shows the size composition of *Nacella concinna* eaten by kelp gulls compared with the size-frequency distribution of the natural population from and a shallow tidal pool. The gulls feed only limpets larger than 20 mm.
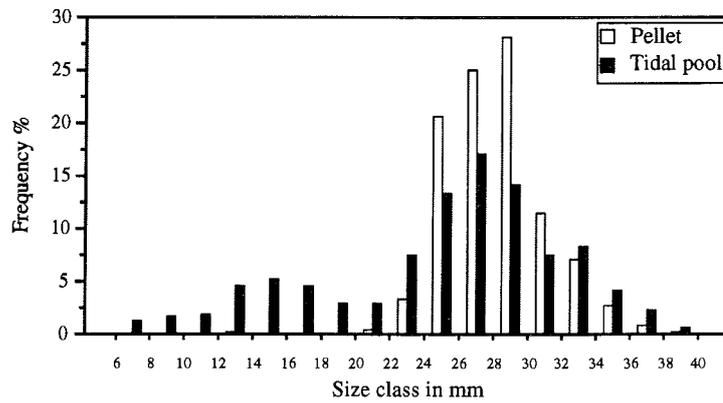
Fig. 4.7. The size-frequency distribution of *Nacella concinna* from pellets regurgitated by *Larus dominicanus*, sampled from the intertidal transect, compared with those from a shallow tidal pool (feeding ground) in November 1997.

4.4. Discussion

I will discuss the population structure of *Nacella concinna* at first and compare, at the same time, two populations of the intertidal and sublittoral limpets. In a next step, I will compare the migratory pattern of *N. concinna* to those of other intertidal gastropods. Finally, some differences of the intertidal and sublittoral populations will be dealt with.

4.4.1. Population structure

The intertidal population of *Nacella concinna* had the following characteristics: (1) limpets smaller than 20 mm in shell size were almost absent (Fig. 4.1) and most individuals were adults, (2) limpets exhibited a distinct size gradient up the shore, and (3) there was a strong female-biased sex ratio, especially in the young population.

The absence of limpets with smaller shell size than 20 mm appears to be primarily concerned with the lack of larval settlement in the intertidal. There was no evidence that the recruitment of *Nacella concinna* directly took place in the intertidal. Neither on open rocks nor in tidal pools small limpets were observed. In contrast, in very shallow but large tidal pools, where an ice foot was not formed, small limpets, including spat, were observed during the austral winter of 1997. Thus, in spite of the occurrence in the intertidal, the small limpets of shallow tidal pools might be regarded as non-migrants because they could be observed all over the year. In the study area, furthermore, a gap between the 18 – 22 mm size class was observed for the limpets in the shallow tidal pools (Fig. 4.7). Though far from proof, limpets between 18 – 22 mm size may be absent, probably because of failure of recruitment during specific years, and limpets under this size may be unable to tolerate the physical stress of the intertidal (see below). Brêthes et al. (1994) also observed a gap around 10 – 15 mm size of sublittoral limpets in the Antarctic Peninsula.

The intraspecific shore-level size gradient has been observed for many other intertidal gastropods (Vermeij 1972, Underwood 1979, Branch 1981). The intraspecific size gradient has been explained by differential growth rates and density-dependent mortality at various tidal levels (Sutherland 1970, Vermeij 1972, Creese 1980 a, Quinn 1988 a), while the maintenance of these patterns has been explained via active migration (e.g., Frank 1965, Bertness 1977, Hobday 1995). The upper limit of limpet distribution is thought to be restricted by the desiccation conditions, thermal stress and osmotic stress (Lewis 1954, Frank 1965, Vermeij 1972, Branch 1975 a, 1981, Sanders et al. 1991, Marshall and McQuade 1992). According to this explanation for the upper limit, small limpets with high surface-to-volume ratios are at a disadvantage compared to large limpets, so small limpets may be restricted to lower levels, leading to a size gradient with increasing tidal level.

In the case of *N. concinna* active migratory behaviour in connection to different tolerance of different limpet size to environmental stress may be the most feasible explanation for the size zonation exhibited because a vertical size gradient was established from the beginning of the upward migration (Fig. 4.2 and Table 4.2). This can be supported by a significant difference in vertical distances moved between small and large limpets of the mark-recapture experiment in spring. During the summer as well as autumn, however, there were no significant differences between small and large limpets. In response to this pattern of migration, the slopes of the shell size gradients on tidal level gradually decreased during the summer (Table 4.2 and Fig. 4.2).

The mean shell size of limpets eaten by the kelp gull *Larus dominicanus* was smaller than that of the intertidal individuals, but larger than that of the shallow tidal pools (Fig. 4.7). Favero et al. (1997) observed in Potter Peninsula near this study area that the number of kelp gulls searching for limpets was inversely correlated with the tidal level. Kelp gulls can feed selectively only on large limpets in the lower intertidal (Fig. 4.7, Silva et al. 1999). Apart from the migratory behaviour, thus, predation of kelp gulls may be partly responsible for the establishment of size gradients of *Nacella concinna*. On the other hand, Hedgpeth (1971) discussed that predation by the kelp gull *Larus dominicanus* is a limiting factor for the intertidal occurrence of *N. concinna*. However, since kelp gulls usually feed

on *N. concinna* in shallow water during spring low tide (Favero et al. 1997, Cadée 1999) and *N. concinna* occurs up to the tidal level of mean high water spring (M.H.W.S.) during summer, the predation of kelp gulls does not explain the vertical distribution and the upper limits of *N. concinna*.

Fretter and Graham (1964) showed that in most dioecious prosobranch molluscs females predominate, especially in older populations. A number of limpets are consecutive hermaphrodites, almost all being protandrous (first male, then female) (see review by Branch 1981). It has been suggested that if the female gains more in fecundity with an increase in size than the male does, then it will pay to be male first and then female (Branch 1981, Wright 1989, Creese et al. 1990, Warner et al. 1996). Furthermore, Morton (1991) suggested that a pronounced female bias is a means to optimise reproductive success, by maximising resource allocation into more energy-demanding oogenesis, in temporally and spatially heterogeneous habitats. In this study, a significant female bias has been demonstrated for the intertidal *Nacella concinna*, especially in young population, whereas the ratio for sublittoral population was approximately 1:1. These results for intertidal *N. concinna* seem to be contrary to expectations because for most limpet species, males predominate in the smaller size classes and females in the larger size classes (Branch 1981). In contrast to most limpet species, however, *N. concinna* does not change its sex (Shabica 1976). In the case of *N. concinna*, therefore, the preponderance of females in intertidal population may be explained only by the migratory behaviour. The bias to be female for intertidal *N. concinna* may be a local adaptation to heterogeneous habitats for optimising reproductive success.

4.4.2. Seasonal pattern of migratory behaviour

The seasonal changes in vertical distribution (Chapter 3) and the mark-recapture experiment (Fig. 4.6) clearly demonstrate seasonal migration of *Nacella concinna*. *N.*

concinna usually stayed below mean low water neap tide during winter, although upward migration occasionally could be observed during the formation of the ice foot. Upward migration into the intertidal began just after receding of the ice foot at the end of October and reached its maximal extension in February. After active upward migration, limpets moved more or less at random. Downward migration in autumn started before the formation of the ice foot in April and May (Fig. 3.10). This seasonal migration of intertidal limpets has been observed in other temperate regions (Frank 1965, Haven 1971, Breen 1972, Branch 1975 a). Most migratory species of the temperate regions progressively move up the shore under moist and cold conditions during autumn, followed by a less obvious downward movement in summer. In contrast to temperate species, however, *N. concinna* entirely migrates from the intertidal to the sublittoral in autumn and back to the intertidal in spring.

Some species of intertidal gastropods migrate up or down the shore during or just before the period of spawning (Fretter and Graham 1962, Williams 1965, Underwood 1973, Ohgaki 1988). In the study area, spawning of *N. concinna* was observed in February (Chapter 5). During the spawning season, *N. concinna* of the intertidal did not show any strong directional movement (Fig. 3.10), and neither changed the vertical distribution (Fig. 4.6c).

Density-dependent vertical migrations of limpets connected to food supply have been well documented, including manipulative studies (Frank 1965, Branch 1975 a, Breen 1972, Stimson and Black 1975, Cubit 1984). In many intertidal limpets, artificial increases of population densities resulted in emigration from these areas of greater density (Frank 1965, Breen 1972, Stimson and Black 1975). Breen (1971) produced similar effects by reducing the availability of food for the intertidal limpet *Acmaea digitalis*. Brêthes et al. (1994) discussed density-dependent vertical migration of *N. concinna* in the Antarctic Peninsula. They suggested that the major part of the recruitment takes place in the sublittoral, and the migration of adults to the intertidal is related to relaxing intraspecific competition in the sublittoral and the availability of benthic microalgae in the intertidal. In this study area, benthic microalgae densely covered the upper part of the intertidal undisturbed by limpets.

It is likely that in response to this benthic food supply, *N. concinna* moved up to the intertidal.

4.4.3. Migrant vs. non-migrant

On Signy Island, the *Nacella concinna* group migrating to the intertidal during summer and the non-migratory sublittoral group can be distinguished by their shell morphology (Walker 1972, Nolan 1991). These authors considered that differences in morphology between the two groups were phenotypic and induced by a combination of physical, biological and behavioural influences. In this study, a significant difference in shell morphology between the intertidal and sublittoral limpets confirms the existence of two sub-groups on King George Island (Fig. 4.5).

In the mark-recapture experiment, a remarkable difference in the migratory behaviour between the intertidal and sublittoral limpets was found (Fig. 4.6a). Wallace (1972) has shown that high-level limpets tolerated for desiccation better than sublittoral specimens of comparable size. Nolan (1991) found that for *Nacella concinna* of similar length, littoral shells have a greater internal volume but contain a lower tissue biomass than those of the sublittoral. It is, at present, unknown whether intertidal limpets with steeper shells may have an advantage in the intertidal environment or whether some other –physiological- acclimation may take place by the regular migration to the intertidal. In any case, if those acclamations occurred, the two sub-populations would be irreversibly separated and the separation would be deeper with increasing age. More information on morphological and physiological acclimation is needed.

Chapter 5

Reproduction of *Nacella concinna*

5.1. Introduction

All organisms live in changing environments; these changes may be regular and relatively predictable, or irregular and unpredictable. In the Antarctic rocky intertidal biological and physical environmental factors, including food supply for *Nacella concinna*, exhibit high seasonality and interannual variation (Chapter 3). *N. concinna* can avoid unfavourable environmental changes by seasonal migration (Chapter 4).

Studies of intertidal gastropods, especially limpets, have found marked intraspecific variations in the population characteristics (Sutherland 1970, Frank 1975, Roberts and Hughes 1980, Fletcher 1984 a, b, Moran et al. 1984, Quinn 1988 a, b). Food is one of the main factors in determining variations. Temporal and spatial variations in the availability of food have been used to explain aspects of behaviour (Mackay and Underwood 1977, Little 1989), morphology (Underwood and Creese 1976) and population dynamics (Sutherland 1970, Creese 1980 a, Parry 1982 a, Workman 1983, Fletcher 1984 a, Quinn 1988 a, b) of intertidal gastropods.

Food limitations can affect a variety of functions such as growth, size, mortality or reproductive potential. Life history theory predicts that heterogeneous environments will favour environmentally sensitive energetic allocation to somatic growth and reproduction (Giesel 1976, Caswell 1983). This phenotypic variation is likely to have important consequences in determining the distribution of species, or their persistence within any area.

Although reproduction biology in *Nacella concinna* was examined at Palmer Archipelago (Shabica 1971, 1976), at Signy Island (Picken 1980) and at the Antarctic Peninsula (Brêthes et al. 1994), there have been no studies in the South Shetland Islands. *N. concinna*

spawns synchronously once a year (Picken 1980, Picken and Allan 1983, Brêthes et al. 1994, Stanwell-Smith and Clarke 1998), and water temperature and food availability are important factors in the reproductive cycle (Shabica 1976, Picken 1980, Stanwell-Smith and Clarke 1998). Maturity occurs in limpets > 20 mm long (7 years old) and the annual reproductive output of *N. concinna* is low in comparison with other Patellidae (Picken 1980). In order to improve understanding of the reproduction biology of *Nacella concinna* in King George Island, seasonal changes in gonad and somatic mass as well as in reproductive effort were investigated. In addition, some aspects of reproduction were compared between two summers in connection with the food availability.

5.2. Material and Methods

Gonad and somatic condition index

All limpets sampled were preserved in a 5 % formaldehyde solution and left for at least 4 weeks to allow the gonads to harden which aids in their dissection (Underwood 1974). Maximal shell length and height was measured to ± 0.1 mm with Vernier Callipers. The relationship between wet and dry tissue weights was determined using 141 males and 142 females which were sampled between December 1996 and February 1997. The tissues were excised and the sex of mature individuals was recorded. Then gonad and somatic tissues were weighed, dried at 60°C for a week, and weighed to ± 0.001 mg. Regressions of dry weight against wet weight of gonad and somatic tissues were calculated. Since the relationship of dry vs. wet weight was highly significant (see Chapter 5.3.2), wet weight was determined only in other individuals and converted to dry weight accordingly.

The condition index and gonosomatic index were used to describe the annual cycle of somatic and gonad tissues. For this purpose, a condition coefficient was calculated, corresponding to the somatic, respectively gonad, mass divided by the cubic value of the maximal shell diameter:

$$SCI = (SDW / SL^3) \times 1000$$
$$GCI = (GDW / SL^3) \times 1000$$
$$GSI = (GDW / SDW) \times 100 \%$$

SCI, GCI and GSI = somatic condition, gonad condition and gonosomatic index respectively

SDW and GDW = dry weight of somatic and gonad mass respectively in mg

SL = shell length in mm

Reproductive effort

It has been suggested by Hirshfield and Tinkle (1975) that reproductive effort is best measured by energy budgets. Parry (1982 b) found that both energy budgets and ratios of gonad to somatic weight gave similar results for four species of limpets. Reproductive effort has been measured for limpets, using gonad to body weight ratios, by Branch (1974), Choat and Black (1979), Picken (1980), Fletcher (1984 b) and Liu (1994). Annual effort put into reproduction is actually the gonad output per annum, e.g., the maximum gonosomatic index minus the minimum.

5.3. Results

5.3.1. Maturity

The size at which reproductive maturity is reached was determined by examining the relationship between gonosomatic index and shell length before and after spawning (January and February 1997, see chapter 5.3.3). In animals above 20 mm there is a marked increase in the relative weights of both testis and ovary (Fig. 5.1), and this is considered to
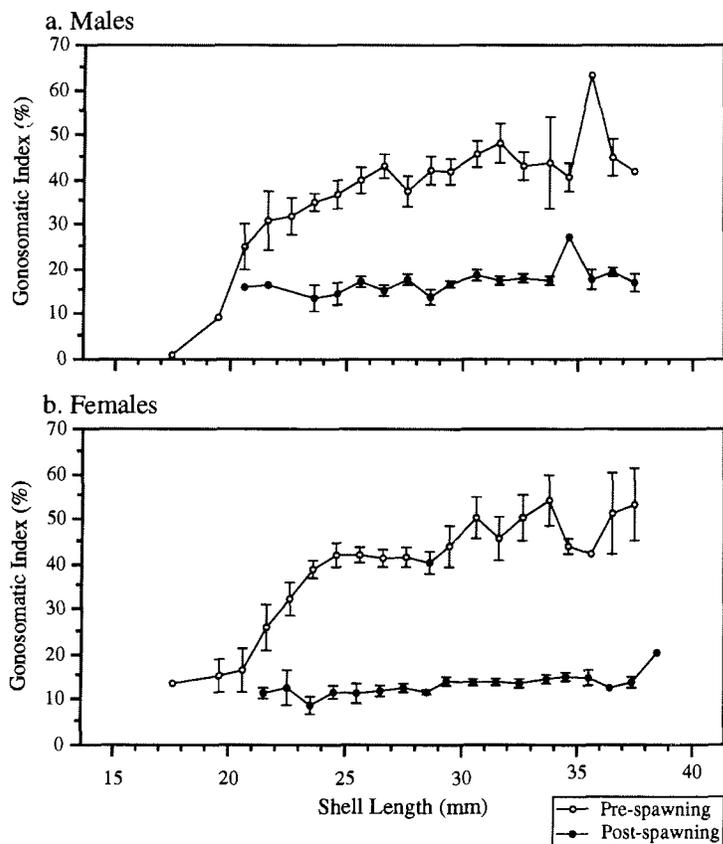
Fig. 5.1. Gonosomatic index for 1 mm size categories of adult males (a) and females (b) of *Nacella concinna*.

indicate the attainment of maturity. Above 26 mm shell size the gonosomatic index was more or less independent of size. There was no evidence that one sex may mature at a smaller size than the other. Thus, most intertidal limpets (99.8 %) were mature. The smallest male with a detectable gonad was 16.9 mm, the smallest female 17.3 mm long.

5.3.2. Relationships between wet/dry tissue weight and tissue weight/shell length

Relationships between wet and dry weight

Table 5.1 shows the relationships between wet and dry weight of limpet tissue. All regressions were highly significant. For somatic tissue, the relationships did not differ significantly between the two sexes (slope and intercept, all $P > 0.05$). For gonad tissue, however, covariance analysis demonstrated significant differences between estimates of the slopes between males and females ($P < 0.001$, Fig. 5.2), indicating that in same sized limpets the testis had higher moisture contents than the ovary.
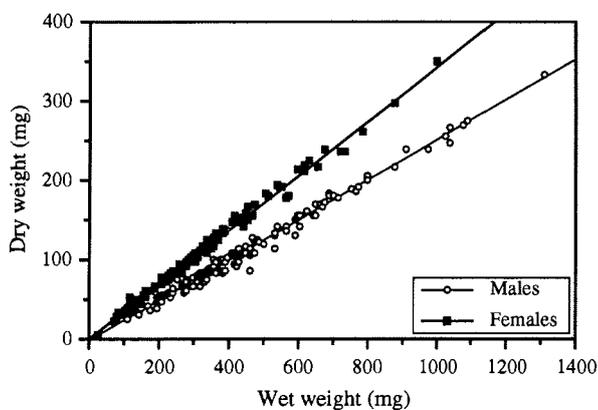
Fig.5.2. The relationship between wet and dry weight of gonads of *Nacella concinna*.

Table 5.1. Regression equations between wet (X; mg) and dry weight (Y; mg) of limpet tissue.

Sex	n	Somatic tissue Regression equation	R^2	Gonad tissue Regression equation	R^2	Total Regression equation	R^2
Male	141	Y = 0.24 X + 3.14	0.95	Y = 0.25 X – 1.41	0.99	Y = 0.24 X + 2.41	0.97
Female	142	Y = 0.24 X + 1.89	0.97	Y = 0.34 X + 0.87	0.99	Y = 0.27 X – 4.97	0.98

Relationships between shell length and tissue weight

All allometric equations of dry somatic tissue weight on shell length were highly significant (see Appendix, Table A-7). Covariance analysis indicated no significant differences in slopes and intercepts of relationships between the two sexes, whereas there were significant difference in slopes and intercepts between the different months (Table 5.2).

On the other hand, allometric equations of dry gonad tissue weight and shell length differed in different months (see Appendix, Table A-7). Regarding gonad weight, analyses of covariance demonstrated significant differences in slopes and intercepts of relationships between the two sexes as well as between the different months (Table 5.2 b). Between

Table 5.2. Full interaction of ANCOVA for dry weight (mg) of somatic (a) and gonad tissue (b) vs shell length (mm) with covariate month and sex. Month and sex are fixed and shell length is variable. Data refer to individuals > 12 mm shell length.

	df	a) Somatic tissue MS	F		b) Gonad tissue MS	F	
Month (M)	11	0.035	10.493	***	0.085	2.347	**
Sex (S)	1	0.001	0.179	ns	0.306	8.474	**
Shell length (L)	1	48.511	14344	***	75.279	2083	***
M x S	11	0.001	0.308	ns	0.036	0.995	ns
M x L	11	0.045	13.181	***	0.080	2.215	*
S x L	1	0.0002	0.046	ns	0.289	7.997	**
M x S x L	11	0.001	0.349	ns	0.036	1.007	ns
Residual	3673	0.003			0.036		

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns is not significant, $P > 0.05$

males and females, there were no difference in the relationships during the first summer,

whereas some significant differences in slopes and intercepts were found during the second

summer (Table 5.3). For most times of sampling during the second summer, the slopes of

the regressions for females were significantly higher than for males. The analyses also

showed significant differences between the intercepts of the regressions for males and

females. In these cases, the small females usually had small gonads in comparison to males

of the same size, while for large size limpets the gonads of females were larger than those

of males.

Table 5.3. Full interaction of ANCOVA for dry weight (mg) of gonad tissue vs. shell length (mm) with covariate month and sex during first summer (a, from December 1996 to April 1997) and during second summer (b, from November 1997 to March 1998). Month and sex are fixed and shell length is variable. Data refer to individuals > 23 mm shell length.

	a) First summer				b) Second summer		
	df	MS	F			MS	F
Month (M)	4	0.141	5.647	***	4	0.051	1.294 ns
Sex (S)	1	0.021	0.845	ns	1	0.316	8.046 **
Shell length (L)	1	25.954	1036	***	1	79.182	2014 ***
M x S	4	0.026	1.023	ns	4	0.046	1.181 ns
M x L	4	0.116	4.629	**	4	0.054	1.380 ns
S x L	1	0.017	0.668	ns	1	0.318	8.092 **
M x S x L	4	0.025	0.986	ns	4	0.048	1.221 ns
Residual	821	0.025			2646	0.039	

* denotes significance $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns is not significant, $P > 0.05$

5.3.3. Seasonal variation in somatic tissue

Since the relationships of somatic tissue and shell length were not different between the

two sexes, the data of males and females were pooled for somatic condition index. Fig.5.3

shows the seasonal variation of somatic condition index for the individuals between 28 and

32 mm shell length. A clear seasonal pattern was observed for the somatic condition index

from December 1996 to November 1997. The somatic condition index increased from

December 1996 and shows maximum values in April 1997. Later, the values rapidly decreased until October 1997. Between October and November 1997, the values of the index slightly increased, but the somatic condition factor collapsed in December 1997 when diatom films entirely disappeared from the intertidal. The mean somatic condition factors were significantly lower during the second summer than during the first summer.

The relationships between somatic tissue weight and shell length are compared between January 1997 and 1998 in Fig. 5.4. The slopes and intercepts of relationships were significantly different between the two summers ($P < 0.001$). For all size classes, the somatic mass of the second summer was smaller than that of the first summer. However, the significant difference in the slopes indicated that for large limpets the difference in somatic tissue weight between the two summers was proportionally greater than for small limpets.
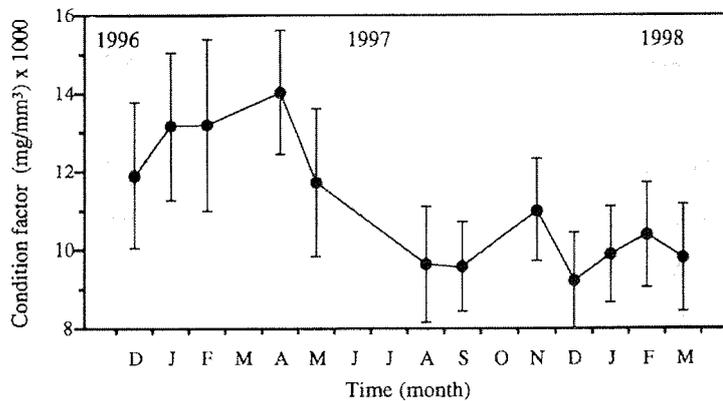
Fig. 5.3. Seasonal variation of the mean somatic condition factors of *Nacella concinna* in the intertidal of King George Island. Vertical bars represent standard deviations. Individuals between 28 and 32 mm were used.
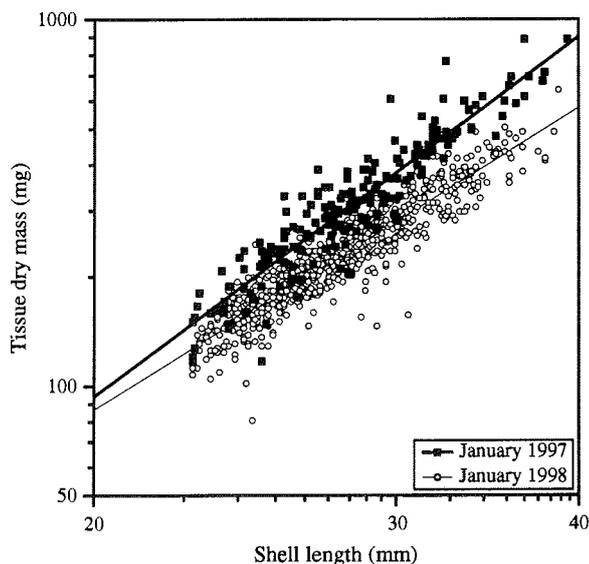
Fig. 5.4. Comparison of relationships of somatic tissue dry weight vs. shell length of *Nacella concinna* between January 1997 and 1998.

5.3.4. Seasonal variation in gonad condition index and timing of spawning

Variations in the gonad condition index for both male and female individuals of intertidal limpets are shown in Fig. 5.5. Both males and females showed a similar gonadal cycle. At the beginning of the study period, the gonad mass increased parallel to the somatic mass and peak maturation was reached in January 1997. The following sharp drop in gonad index indicated the liberation of gametes in February 1997. In contrast to the somatic condition index, after spawning ovary and testis developed continuously without resting period during winter. In spite of increasing constantly until January 1998, the gonad condition index was significantly lower during the second summer than during the first summer regarding January values. Although spawning was observed in a small number of individuals in February 1998, the main reproduction event did not occur before March 1998.

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The relationships of dry gonad tissue weight and shell length are compared between January 1997 and 1998 in Fig. 5.6. The relationships in male limpets did not differ between the two summers. In contrast to males, the slopes and intercepts of relationships in females were significantly different between the two summers ($P < 0.001$). Small females of the second summer appear to have smaller gonad than those of the first summer while the gonads in large females were approximately of the same size.
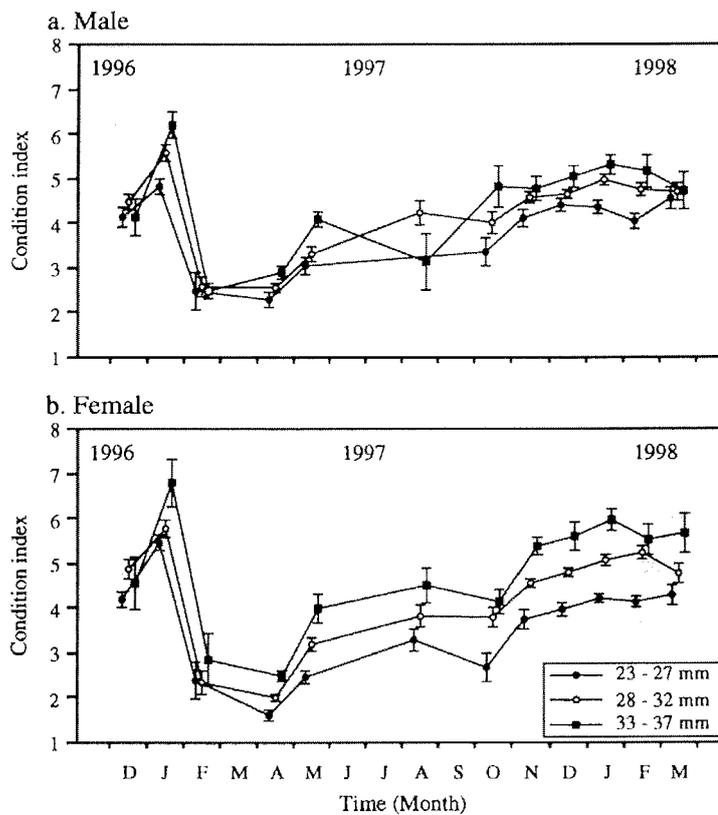
Fig. 5.5. Seasonal variation of the mean gonad condition index of *Nacella concinna* in the intertidal of King George Island. Vertical bars represent standard errors.
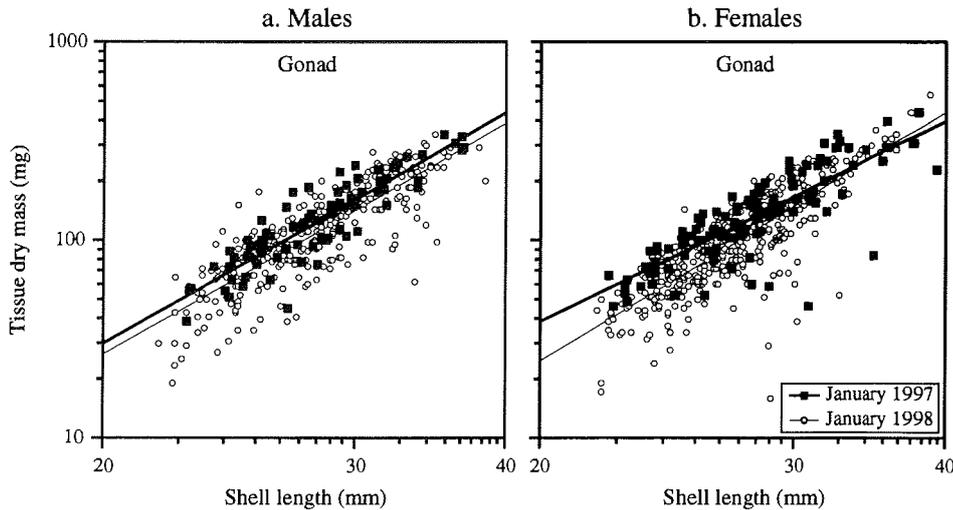
Fig. 5.6. Comparison of relationships of dry gonad tissue weight vs. shell length in *Nacella concinna* between January 1997 and 1998.

5.3.5. Gonosomatic index and reproductive effort

Gonosomatic index

The gonosomatic index showed a similar cycle as the gonad condition index (Fig. 5.7). Unlike the gonad condition index, however, the values of the gonosomatic index for large limpets were much higher during the second summer than during the first summer. During the first summer, the gonosomatic index prior to spawning (January 1997) did not correlate with shell size and mean values were 42.5 % and 44.2 % for males and females, respectively. In contrast, during the second summer, the gonosomatic index increased with increasing shell size. In January 1998, for example, the values rose for male limpets from 42.5 % (23-27 mm) to 56.6 % (33-37 mm) and those for females increased from 38.5 % (23-27 mm) to 65.0 % (33-37 mm). The gonosomatic indices of January 1997 and 1998 are compared in Fig. 5.8. In January 1997, the values increased with shell length to a

maximum value and then slightly decreased, and were not different between the two sexes. These decreases probably occur because the equations from which the ratios are derived are increasingly inaccurate at large shell lengths. For large limpets, both males and females, the values of the second summer were higher than those of the first summer. For females in particular, the index did not reach a maximum value, but continuously increased with increasing shell size.
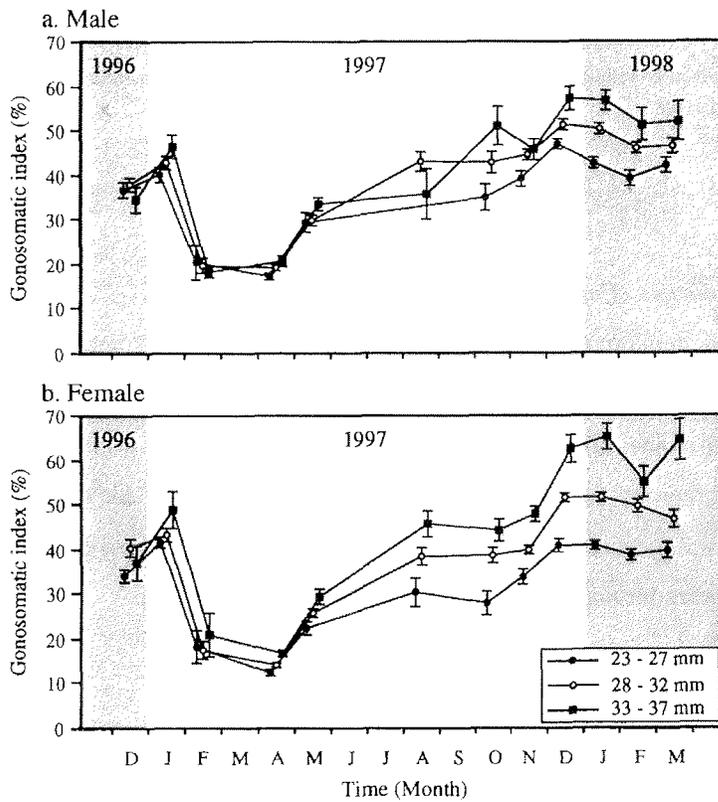
Fig. 5.7. Seasonal variation of the mean gonosomatic factors of *Nacella concinna* in the intertidal of King George Island. Vertical bars represent standard errors.
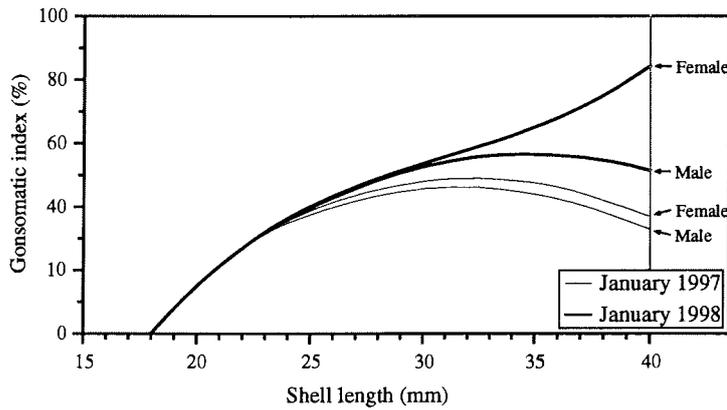
Fig. 5.8. Comparison of relationships of gonosomatic index vs. shell length in *Nacella concinna* between January 1997 and 1998.

Annual reproductive effort

Since *Nacella concinna* spawns once a year and this occurred between January and February 1997, the differences between the gonosomatic values of pre- and postspawning were taken for annual effort put into reproduction. Female *N. concinna* demonstrated a greater annual reproductive effort (30.8 %) than males (25.3 %). This difference was due to the postspawning values. After spawning, the gonads do not regress completely and the gonosomatic index for males was higher than for females ($t < 0.05$).

5.4. Discussion

Somatic and gonad condition index showed a clear seasonal pattern from December 1996 to November 1997. After that, *Nacella concinna* underwent a severe food shortage (see Chapter 3) which directly reflected the gonad and somatic condition. Therefore, I will discuss a seasonal pattern in the development of gonad and somatic mass, including spawning time, at first. Then, I compare some aspects of reproduction between the two summers in relation to food availability.

5.4.1. Seasonal development of gonad and somatic tissue

Somatic condition index showed a clear seasonal pattern between December 1996 and November 1997. Maximum tissue weights were recorded before and after the spawning season (January-April), and minimum tissue weights were found during winter (August-October). The seasonal cycle of the somatic condition index appears to be coupled to the food availability. Filamentous algae and benthic diatoms were abundant in the intertidal until April 1997 (Chapter 3). This high food supply during summer was reflected by an increase of the somatic mass. During the period of food shortage in winter, the somatic mass declined steadily until the microphytobenthic bloom occurred in the following spring. In contrast to the summer 1996/97, filamentous algae and benthic diatoms developed poorly in the early spring 1997/98 and disappeared in December 1997 entirely (Chapter 3). This food shortage seems to be directly reflected in a collapse of the somatic condition index in December 1997. The somatic condition index increased slightly in the course of the second summer, but it was substantially lower than in the first summer. Brêthes et al. (1994) observed a similar seasonal pattern in *Nacella concinna* of Esperanza Bay (Antarctic Peninsula) and they found that the variations in somatic mass were directly related to microphytobenthos availability.

Seasonal development of gonad mass seems to be coupled less to food supply. After spawning in February, gonad mass progressively developed without resting period during the winter. Even when the somatic condition index collapsed during the second summer, gonad mass steadily increased. Therefore, it can be suggested that energy was channelled into reproduction from storage tissue for reserves. Simpson (1982) observed a transfer of lipids from the digestive gland to the gonad during the reproductive cycle in *Nacella macquariensis*. A sustained increment in the gonad mass could be supported, in part, at the expense of somatic mass.

Nacella concinna appears to spawn once a year, in agreement with the observations in other Antarctic regions (Shabica 1976, Picken 1980, Picken and Allan 1983, Brêthes et al. 1994). On King George Island, however, *N. concinna* seems to spawn much later (in February) whereas in other Antarctic regions spawning was observed between November and January. In addition, during the summer 1997/98, spawning in the intertidal population was delayed and the main reproduction event was not observed before March 1998, whereas the sublittoral limpets spawned in February 1998 (D. Kim, unpublished data).

The spawning of intertidal limpets has been ascribed to be stimulated by changes in temperature (Fritchman 1962) and by wave action (Orton et al. 1956, Bowman and Lewis 1977, Thompson 1980). Previous workers (Shabica 1976, Picken 1980) in Antarctica have proposed that the proximate environmental cue for spawning in *Nacella concinna* is temperature and that spawning occurrs about 3 weeks after the coastal sea-water temperature rose to – 1.4°C. The rise in water temperature seems not to be cue for the spawning in *N. concinna* on King George Island because the sea-water temperature reached maximum and rose over + 1°C in January (Kang et al. 1997). In a more recent study at Signy Island, Stanwell-Smith and Clarke (1998) found that there was little correspondence between the the spring increase in seawater temperature and the timing of spawning of *N. concinna* by summarising the data over nine separate years. Furthermore, they suggested that reproduction in *N. concinna* is triggered by the spring phytoplankton bloom. Studies of reproductive cycles of marine invertebrates have shown that times for

peak maturation, spawning, and resting stages can differ markedly between successive years (e.g., Orton et al. 1956, Underwood 1974, Stanwell-Smith and Clarke 1998) and with locality. Such findings indicate that events within the reproductive cycle are susceptible to environmental influence. Light, salinity, temperature, and food may be possible mechanisms for controlling the reproductive cycle of *N. concinna*.

Branch (1974) reported that males of *Patella* spp. from South Africa have a greater gonadal output than females. Liu (1994) obtained similar results in *Cellana grata* and *Patelloida pygmaea* on rocky shores in Hong Kong. However, this is probably due to use of wet weight rather than dry weight. In this study, a significant difference in the relationships of dry vs. wet weight of gonad between males and females indicated that testes have a higher moisture content than ovaries. In terms of wet weight a testis was much heavier than an ovary of a same sized limpet, but the gonad dry weights of both sexes were approximately the same. Similar results were obtained in two species of *Acmaea* (Choat and Black, 1979) and *N. concinna* in Signy Island (Picken 1980). In addition, Parry (1982 b) found that the energy content per unit dry weight is higher in the ovary than in the testis for four species of Australian limpets. In addition, Simpson (1982) found that much more lipid was accumulated in the ovary than in the testis (almost double the amount in the ripe condition) during gonadal development for *N. macquariensis*. In *N. concinna*, therefore, it is likely that females have a greater gonadal output in terms of energy content than males.

5.4.2. Reproductive strategy related to food availability

In this study, the limpets have higher dry gonad mass to total dry mass ratios prior to spawning ($\approx$ 30 % in January 1997) than those at Signy Island ($\approx$ 15 %, Picken 1980) and those on the Antarctic Peninsula ($\approx$ 10 %, Brêthes et al. 1994). Where intraspecific variation has been investigated, many studies have found large differences in the

reproduction effort among populations inhabiting different areas (e.g., Branch 1974, Snell and King 1977, Hughes and Roberts 1980, Stearns 1980, Brown 1983, Fletcher 1984 b, 1987).

Increased fecundity with increased size or age is usual for marine invertebrates in general (e.g., Barnes and Barnes 1968, Sameoto 1971, Gonor 1972, Creaser 1973, Rutherford 1973, Wyatt 1973, Menge 1974, Thompson 1979) and for molluscs in particular (e.g., Branch 1975 b, Choat and Black 1979, Roberts and Hughes 1980, Hart and Begon 1982, Perron 1983, Quinn 1988 b). Therefore, most species can potentially adjust fecundity to increasing food supply by growing (Spight and Emlen 1976, Quinn 1988 b, Guilou and Lumingas 1999). However, there are many instances where animals are known to put additional resources into reproduction when food is abundant; e.g., gastropods (Spight and Emlen 1976, Fletcher 1984 b) and copepods (Uye 1981, Kimmerer 1984).

In *Nacella concinna*, gonad dry weight increased with size (and therefore age) both in males and females. In male *N. concinna*, gonad output seems to be independent of the food supply, when the relationships of gonad dry weight on shell length are compared between the two summers. The small females had smaller gonads under food limited conditions during the second summer, but gonad dry weights in large females were approximately the same in the two summers. Thus, *N. concinna* seems to be more flexible in growth rate rather than in reproduction because the reduced food supply had a greater effect on somatic production than on reproductive output.

The reproductive effort of an individual or species may increase allometrically with age (Williams 1966, Gadgil and Bossert 1970, Kaplan and Salthe 1979, Bayne et al. 1983, Thompson 1984). Fletcher (1984 b) found that the reproductive effort of *Cellana* did not vary over the range of adult sizes and showed no tendency to increase with age. During the summer 1996/97, gonad to body ratios increased with shell length following the attainment of sexual maturity, but approached a maximum value at large shell lengths. Similarly, the proportion of body weight invested in gonads is independent of shell length in all but the

smallest adults in the Antarctic limpet (Picken 1980). This results is not uncommon in gastropods, similar results have been found in limpets (Creese 1980 b, Branch 1974, Picken 1980), in four species of *Conus* (Perron 1982) and in muricids (Spight and Emlen 1976).

In contrast to the first summer, the gonosomatic index increased significantly with increasing shell size under limited food conditions during the second summer. This increment in gonosomatic index was more evident in females than in males. The gonosomatic indices in small limpets were not different between the two summers, whereas the values of the indices in large limpets were much higher during the second summer than during the first summer. In females, the mean values of the gonosomatic index increased steadily with size from 40 % to 60 % during the second summer. Although the gonad output did not change when food resources were scarce, reproductive effort in *Nacella concinna* may have been enhanced (see also Calow and Woollhead 1977, Bayne et al 1978, Hirshfield 1980, Thompson 1983). This evidence supports the result that reproductive effort is not constant within a population (Fletcher 1984 b). Fletcher (1984 b) has shown that the amount of environmentally determined variation in the reproductive output of the limpet *Cellana tramoserica* exceeds interspecific differences.

Reproduction may be risky (Grahame and Branch 1985). Life history theory suggests that energy allocated to reproduction reduces the amount of energy available for maintenance and reproductive efforts should be positively correlated with the rate of extrinsic adult mortality, e.g., the mortality that would occur irrespective of the level of reproductive effort (Hirshfield and Tinkle 1975). Parry (1982 a) using four intertidal limpets as examples, demonstrated that the adults of species which occur in seasonal environments appear to take greater risks when breeding than those of species which occupy more constant environments. In December 1997 and January 1998, a number of dead limpets, most likely not subject to predation (remaining soft tissue in shell), were found (D. Kim, person. observ.). Under food limited conditions of the second summer, the values of gonosomatic index increased with increasing shell size and exceeded 60 % for the large females. Therefore, a high mortality for the large limpets, especially for females, may be

expected during the second summer. Since the large females appear to put more effort into reproduction than males under food limited conditions, this may result in a higher mortality of the former and may lead to a decrease in the proportion of large females in the intertidal part of the *N. concinna* population.

Chapter 6

General discussion

In this chapter, I will discuss at first the possible factors which can affect the seasonal development of the intertidal algae. In the next step, I will deal with the seasonality of *Nacella concinna*. This will be including seasonal migration, comparison in population characteristics between the intertidal migrant and sublittoral non-migrant, and life history patterns related to food availability.

The natural distribution and abundance of algal cover can be influenced by several factors. The seasonal development of algae is generally triggered by physical factors, such as light, temperature and/or nutrient conditions (Chapman and Craigie 1977, Lüning 1980, Lüning and tom Dieck 1989, Wiencke 1996). An important feature which distinguishes the shallow water marine ecosystem around Antarctica from those elsewhere in the world is the impact of ice (Clarke 1988). Except for the ice disturbances, this study demonstrated that the distribution and abundance of the Antarctic intertidal algae could be controlled by grazing of *Nacella concinna*, at least in the lower part of the shore (Chapter 3). In addition, other grazers, such as *Laevilittorina* sp. and amphipods, are abundant in the Antarctic intertidal (Castilla and Rozbaczylo 1985, Rauschert 1991, Iken 1996) and their role on development of intertidal algae requires further investigation.

The physical factors affect the abundance of species not only through mortality caused by stress, but also through generating annual cycles in rates of primary production (Cubit 1984). On the other hand, ice disturbance and grazing by *N. concinna* may reduce the standing stock of the intertidal algae through mortality. Since the impact of ice and grazing by *N. concinna* varied with season, the seasonal fluctuation in algal cover could be explained by variations in rates of physical and biological disturbances, in rates of production by the algae, or by a combination of the two.

Except for the seasonal variation, the physical and biological factors can vary with tidal levels (Chapter 3). The importance of biotic factors in controlling the distribution and

abundance of marine organisms is generally thought to decrease with increasing level in the intertidal zones of rocky shores. Consistent with this perspective, algal abundance has been shown to be influenced by competition and herbivory at lower intertidal levels, while at upper intertidal levels algal abundance appears to be governed principally by physical stress (Aleem 1950, Lawson 1957, Castenholz 1961, Lewis 1964, Chapman 1973, Haven 1973, Underwood 1980, 1981). This seems to be correct in the intertidal zones of Antarctic rocky shores because frequency and intensity of ice disturbance and physical stress increased with increasing tidal level, whereas influence of grazing by *Nacella concinna* is usually restricted to the lower intertidal.

Previous observations and experimental works have proposed that early life stages are of critical importance for population dynamics of bloom-forming macroalgae on rocky shores (Hruby and Norton 1979, Lubchenco 1983, Vadas et al. 1992) and on soft bottoms (Schories 1995, Lotze 1998). In general, early life stages are more sensitive to environmental change or herbivore pressure compared to adults (Lotze 1998). In the study area, the recruitment of most intertidal algae occurred only in early spring (between October and November), except for *Acrosiphonia arcta* and *Porphyra endiviifolium*. In spite of the fluctuation of their abundance, the pattern of vertical algal distribution in early spring remained until later summer. Therefore, development of early stages into adults may be important to determine later population development and species dominance patterns. The development of early stages in the beginning of the vegetation period seems to be dependent on abundance in the propagule bank, timing of the receding ice foot and other physical conditions, such as temperature, light climate and nutrients.

The initiation of algal recruitment in early spring originated from overwintering propagules. Abundance in the propagule bank may be primarily related to the total reproductive output (Schories 1995, Lotze 1998), and be affected by disturbance owing to grazing and the winter ice foot. Clearly additional experimental work on this subject is required. Timing and rate of germination appeared to be controlled by temperature and light climate after receding of the ice foot in early spring. Further population development into adults and the potential for forming a mass bloom depend on the relative impact of nutrients (Lotze 1998), losses to herbivory and ice scouring in germlings and adults. In the

Antarctic, although concentrations of the major nutrients are high and non-limiting for macroalgal growth throughout the year (Drew and Hastings 1992), Wiencke (1996) noted that studies on micronutrient limitation of Antarctic macroalgae are needed. Disturbance by ice scouring usually was severe in early spring, but floating ice occurred occasionally and disturbed the intertidal in summer. As a consequence, most macroalgae which recruited in early spring showed a patchy distribution and the degree of patchiness increased in the course of summer. The space opened by ice disturbance was rapidly covered by fast-growing opportunistic filamentous algae and benthic diatoms. Herbivore pressure by *Nacella concinna* was less severe on adults compared to early life stages, which again demonstrated the vulnerability of early stages as proposed by Vadas et al. (1992). However, *N. concinna* heavily consumed filamentous algae and benthic diatoms. Because of upward migration and grazing *of N. concinna*, barren space gradually increased at lower intertidal levels in the course of summer. On the other hand, coverage of filamentous algae and benthic diatoms extended at high intertidal levels without grazing by *N. concinna*. Therefore, herbivore grazing seems to limit the distribution and abundance of Antarctic intertidal algae at low shore levels, whereas physical factors including ice disturbance seem to control algal growth at the upper shore levels.

The results of this study indicate a large interannual variation in the distribution and abundance of the intertidal algae. An ENSO (El Niño Southern Oscillation) influence on the recolonisation of benthic fauna in Antarctic shallow water has been suggested (Dayton 1989, Rauschert 1991). Although the data from this study were collected in an El Niño year, the results do not permitted final conclusions concerning an ENSO impact on Subantarctic benthos recolonization. Further long-term studies and experimental work are needed.

It is clear that seasonal migration of *Nacella concinna* is an adaptation to the Antarctic intertidal (Walker 1972). It avoids the severe effects of the winter climate by movement into the sublittoral, and gradually migrates to the intertidal, grazing the filamentous algae and benthic diatoms in spring. The upward migration seems to be dependent upon the individual size because limpets obviously exhibited a size gradient with increasing tidal

level (Chapter 4). The upper limit of limpet distribution is thought to be restricted by desiccation conditions, thermal stress and osmotic stress (Lewis 1954, Frank 1965, Vermeij 1972, Branch 1981, Sanders et al. 1991, Marshall and McQuade 1992). According to this explanation for upper limits, small limpets with high surface-to-volume ratios are at a disadvantage compared to large limpets, so small limpets may be restricted to lower levels, leading to a size gradient with increasing tidal level. However, the greater proportion of limpets never appears to leave the sublittoral zone (Walker 1972). There are distinct morphological differences between the migrants and non-migrants in *N. concinna* (Walker 1972, Nolan 1991, see also Chapter 4). The intertidal migrants had a larger height/length ratio and the shells lacked epibiontic fauna. Furthermore, mark-recapture experiments indicated a difference in migratory behaviour between the two sub-groups (Chapter 4). Since a study of alletic variation revealed no discernible difference between the two forms at Signey Island (Beaumont and Wei 1991), it is suggested that the intertidal migrants are morphologically or physiologically acclimated to the intertidal environment. If this assumption is correct, the individuals adapting to the intertidal may migrate regularly. However, we need more information on the adaptation.

Studies of intertidal gastropods, especially limpets, have revealed marked intraspecific variations in the population characteristics in a number of species (Sutherland 1970, Branch 1975 b, Lewis and Bowman 1975, Choat 1977, Thompson 1980, Creese 1980 b, Workman 1983, Fletcher 1984 a, b). In addition, large differences have been found between intertidal and sublittoral populations for *Cellana tramoserica* (Fletcher 1984 b). This study demonstrated that adult individuals only were found in the intertidal and there were considerable differences in sex-ratio between the intertidal migrants and the sublittoral non-migrants. Although it is difficult to compare directly, the gonosomatic index was much higher in the intertidal limpets of King George Island than in the sublittoral limpets of Esperanza Bay (Brêthes et al. 1994) and of Signy Island (Picken 1980). Furthermore, Brêthes et al. (1994) noted that differential growth between two sub-groups might be possible. Taken together, it can be presumed that the population characteristics in the Antarctic limpet are largely different between the intertidal and sublittoral group.

Apart from the differences among habitats, limpets may encounter a variety of environmental conditions. To resist unfavourable environmental changes and to improve survival, limpets can modify their pattern of resource allocation to growth, maintenance and reproduction. Chapter 3 showed that the distribution and abundance of the intertidal algae exhibited a high seasonality and interannual variation. Food is one of the main factors in determining variations in limpet growth and reproduction (e.g., Quinn 1988 a, b). Food limitation led to a reduction in the somatic condition factor in *Nacella concinna*. Unlike the somatic, the gonad condition factor continuously increased in food-limited conditions during the second summer. Thus, it can be inferred that *N. concinna* is more flexible in growth rate rather than reproduction with respect to the fluctuation of food supply. In consequence, the value of relative reproductive effort was higher under food-limited conditions during the second summer compared to the first summer. In particular, the reproductive effort exceeded 60 % in the large females and this high reproductive effort appeared to lead to adult mortality.

In conclusion, for the Antarctic intertidal algae the relative importance of physical factors (predominantly ice impact, light, temperature and nutrient) versus biological factors such as grazing by the Antarctic limpet *Nacella concinna* varies with season and with tidal levels. This variation leads to characteristic seasonal changes in the distribution and abundance of the intertidal species. The seasonal migration of *N. concinna* is an adaptation to severe environmental condition in the Antarctic intertidal. Environmental factors, and especially food availability, appear to play an important role in the life cycle of the intertidal *N. concinna*. Limpets seem to be very sensitive to food availability, but to be more flexible in growth rate rather than reproduction. The different environmental conditions between the intertidal and sublittoral appear to lead to intraspecific variation in life history traits of *N. concinna*.

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Appendix

Tab. A-1. `Nail mortality´ (Chapter 3.3.2.1)

Mean mortality (%) with standard errors. n = number of wooden plates (see Chapter 3.2.1).

Month	n	Mean ± SE	
		M.H.W.N.	M.L.W.N.
February 1997	8	30.2 ± 9.43	3.0 ± 1.31
March 1997	8	97.0 ± 2.00	43.8 ± 16.6
April 1997	5	92.8 ± 3.38	6.8 ± 4.18
October 1997	8	85.0 ± 9.62	2.5 ± 2.50
November 1997	48	51.7 ± 6.32	18.0 ± 4.02
December 1997	32	5.7 ± 2.95	0
January 1998	40	21.7 ± 5.00	3.3 ± 1.66
February 1998	8	5.0 ± 3.36	0

Tab. A-2. Mean percentage cover (± standard errors) of canopy space (Chapter 3.3.2.3)

Adenocystis utricularis

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	1.1 ± 1.11	12.8 ± 3.15	8.9 ± 2.68	20.6 ± 4.34	10.6 ± 1.02	15.0 ± 9.95	18.9 ± 8.01
Jan 1997	6	2.2 ± 1.65	2.2 ± 1.11	13.3 ± 2.98	29.4 ± 7.95	13.9 ± 4.90	2.8 ± 1.34	36.7 ± 6.67
Feb 1997	6	2.2 ± 1.65	2.2 ± 1.11	33.9 ± 7.52	31.1 ± 11.9	7.2 ± 3.27	3.9 ± 1.59	30.0 ± 3.44
Apr 1997	6	3.9 ± 1.59	3.9 ± 2.18	24.4 ± 4.10	18.9 ± 6.87	1.7 ± 1.14	2.2 ± 1.11	25.6 ± 5.14
May 1997	6	1.1 ± 1.11	3.3 ± 0.86	22.2 ± 5.82	6.1 ± 3.03	0	1.7 ± 1.14	12.2 ± 2.81
Oct 1997	8	Ice-foot	0	1.5 ± 0.84	1.8 ± 1.25	2.6 ± 1.32	2.0 ± 0.67	13.3 ± 2.96
Nov 1997	8	0	0	1.0 ± 0.67	2.8 ± 1.96	4.1 ± 2.15	4.6 ± 1.07	15.6 ± 3.38
Dec 1997	8	0	0	0	6.1 ± 3.11	6.6 ± 2.69	3.1 ± 1.02	23.0 ± 5.10
Jan 1998	8	0	0	0	7.1 ± 3.51	6.6 ± 1.27	6.6 ± 2.00	18.4 ± 3.78
Feb 1998	8	0	0	0	9.2 ± 4.41	11.7 ± 4.67	8.4 ± 1.95	24.0 ± 2.43

Iridaea cordata

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0	0	1.7 ± 1.14	8.9 ± 4.01	27.8 ± 7.78	1.7 ± 1.14	24.4 ± 11.0
Jan 1997	6	0	0	0	1.1 ± 0.70	2.8 ± 1.81	0	10.6 ± 4.82
Feb 1997	6	0	0	0	1.7 ± 1.14	0	0.6 ± 0.56	13.3 ± 5.09
Apr 1997	6	0	0	0	0	0	0	10.0 ± 3.85
May 1997	6	0	0	0	0	4.4 ± 2.05	1.1 ± 1.11	9.4 ± 3.98
Oct 1997	8	Ice-foot	0	0.5 ± 0.51	2.6 ± 1.76	9.7 ± 3.63	4.3 ± 1.83	11.2 ± 3.34
Nov 1997	8	0	0	0.8 ± 0.77	3.6 ± 2.34	7.1 ± 2.67	4.1 ± 1.49	15.6 ± 6.87
Dec 1997	8	0	0	0	2.8 ± 2.00	7.4 ± 3.43	2.8 ± 1.15	7.4 ± 2.34
Jan 1998	8	0	0	0	4.3 ± 2.87	5.4 ± 2.73	2.8 ± 1.22	8.7 ± 2.85
Feb 1998	8	0	0	0.3 ± 0.26	3.8 ± 3.28	4.8 ± 3.16	5.9 ± 4.47	10.5 ± 4.13

Palmaria decipiens

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0	0	9.4 ± 3.38	48.9 ± 6.54	3.3 ± 1.72	2.8 ± 1.81	7.8 ± 4.10
Jan 1997	6	0	0	3.3 ± 1.22	0.6 ± 0.56	1.7 ± 1.67	1.1 ± 0.70	4.4 ± 1.86
Feb 1997	6	0	0	0	0.6 ± 0.56	0	2.2 ± 1.41	0
Apr 1997	6	0	0	0	0	0	0	0
May 1997	6	0	0	0	0	0	0	0
Oct 1997	8	Ice-foot	0	0	0	0	0	0
Nov 1997	8	0	0	0	0	0	0	0
Dec 1997	8	0	0	0	0	0	0	0
Jan 1998	8	0	0	0	0	0	0	0
Feb 1998	8	0	0	0	0	0	0	0

Monostroma hariotii

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0.6 ± 0.56	18.9 ± 3.82	61.7 ± 10.2	91.7 ± 4.77	12.2 ± 3.82	26.1 ± 6.11	4.4 ± 2.05
Jan 1997	6	0	5.6 ± 3.06	21.7 ± 3.31	21.1 ± 4.61	17.8 ± 4.69	0.6 ± 0.56	13.9 ± 3.49
Feb 1997	6	0	1.1 ± 0.70	18.3 ± 4.53	11.7 ± 4.85	4.4 ± 2.05	0	5.0 ± 2.40
Apr 1997	6	0	1.1 ± 0.70	5.0 ± 1.67	0	0	0	2.2 ± 1.41
May 1997	6	0	0	0	0	0	0	0
Oct 1997	8	Ice-foot	0	0	0	0	0	0
Nov 1997	8	0	0	0	0.5 ± 0.50	0	0.5 ± 0.33	0
Dec 1997	8	0	0	0	0	0	0	0.3 ± 0.25
Jan 1998	8	0	0	0	0	0	0	0
Feb 1998	8	0	0	0	0	0	0	0

Porphyra endiviifolium

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0	0	0	0	0	0	0
Jan 1997	6	0.5 ± 0.50	0	0	0	0	0	0
Feb 1997	6	2.2 ± 1.64	0	0	0	0	0	0
Apr 1997	6	10.0 ± 3.45	9.5 ± 3.69	13.3 ± 6.14	0	0	0	0
May 1997	6	2.8 ± 1.40	0.5 ± 0.50	1.7 ± 1.17	0	0	0	0
Oct 1997	8	Ice-foot	0	0	0	0	0	0
Nov 1997	8	0	0	0	0	0	0	0
Dec 1997	8	0	0	0	0	0	0	0
Jan 1998	8	0	0	0	0	0	0	0
Feb 1998	8	0	0	0	0	0	0	0

Acrosiphonia arcta

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0	0	0	0	0	0	0
Jan 1997	6	0	10.0 ± 4.82	3.3 ± 1.28	0.5 ± 0.50	0	0	0
Feb 1997	6	0	6.0 ± 2.00	5.0 ± 1.90	1.2 ± 1.17	0	0	0
Apr 1997	6	0	6.7 ± 1.91	1.7 ± 1.17	1.2 ± 1.17	0	0	0
May 1997	6	0	0	0.5 ± 0.50	0	0	0	0
Oct 1997	8	Ice-foot	0	0	0	0	0	0
Nov 1997	8	0	0	0	0	0	0	0
Dec 1997	8	0	0	0	0	0	0	0
Jan 1998	8	0	0	0	0	0	0	0
Feb 1998	8	0	0	0	0	0	0	0

Tab. A-3. Mean percentage cover (± standard errors) of primary space (Chapter 3.3.2.3)

Adenocystis utricularis

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0.6 ± 0.56	10.6 ± 3.03	7.8 ± 2.38	14.4 ± 3.18	11.1 ± 6.87	10.0 ± 0.86	18.3 ± 7.84
Jan 1997	6	1.1 ± 0.70	1.1 ± 1.11	7.2 ± 2.18	21.1 ± 5.21	12.8 ± 4.82	1.1 ± 0.70	27.2 ± 3.49
Feb 1997	6	1.7 ± 1.14	1.1 ± 1.11	30.0 ± 6.78	27.8 ± 12.0	3.9 ± 1.81	1.7 ± 0.75	10.0 ± 1.49
Apr 1997	6	1.7 ± 0.75	3.3 ± 2.28	20.6 ± 3.59	11.7 ± 4.77	1.1 ± 1.11	1.1 ± 0.70	15.0 ± 3.07
May 1997	6	0.6 ± 0.56	2.22 ± 0.70	20.0 ± 6.33	4.4 ± 2.22	0	1.7 ± 1.14	8.9 ± 2.68
Oct 1997	8	Ice-foot	0	0.8 ± 0.54	1.0 ± 0.77	1.3 ± 1.02	0.8 ± 0.37	5.1 ± 2.31
Nov 1997	8	0	0	0.8 ± 0.54	0.5 ± 0.51	1.3 ± 0.77	0.8 ± 0.37	6.4 ± 2.42
Dec 1997	8	0	0	0	4.1 ± 1.97	2.3 ± 0.90	1.0 ± 0.77	6.9 ± 1.93
Jan 1998	8	0	0	0	4.8 ± 2.56	1.8 ± 0.60	2.6 ± 0.93	5.9 ± 1.36
Feb 1998	8	0	0	0	4.8 ± 2.64	4.1 ± 1.59	3.6 ± 1.43	8.2 ± 1.39

Iridaea cordata

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0	0	1.1 ± 1.11	7.2 ± 3.59	0	5.0 ± 2.24	6.1 ± 3.03
Jan 1997	6	0	0	0	0.6 ± 0.56	1.7 ± 1.14	0	3.3 ± 1.72
Feb 1997	6	0	0	1.1 ± 0.70	0	0.6 ± 0.56	0	9.4 ± 3.79
Apr 1997	6	0	0	0	0	0	0	4.4 ± 1.11
May 1997	6	0	0	0	0	4.4 ± 2.05	0	0.6 ± 0.56
Oct 1997	8		0	0	1.5 ± 0.84	3.3 ± 1.22	1.5 ± 0.64	2.8 ± 0.94
Nov 1997	8	0	0	0	0.3 ± 0.26	2.6 ± 1.14	1.5 ± 0.64	4.6 ± 1.88
Dec 1997	8	0	0	0	0.8 ± 0.54	3.8 ± 1.70	2.3 ± 1.19	5.9 ± 1.74
Jan 1998	8	0	0	0	2.6 ± 1.48	3.1 ± 1.39	1.3 ± 0.66	6.1 ± 1.97
Feb 1998	8	0	0	0	2.6 ± 2.03	3.1 ± 2.22	3.3 ± 2.21	5.1 ± 1.89

Palmaria decipiens

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0	0	1.7 ± 1.67	5.6 ± 1.86	0	0.6 ± 0.56	0
Jan 1997	6	0	0	0	0	0	0	0
Feb 1997	6	0	0	0	0	0	0	0
Apr 1997	6	0	0	0	0	0	0	0
May 1997	6	0	0	0	0	0	0	0
Oct 1997	8	Ice-foot	0	0	0	0	0	0
Nov 1997	8	0	0	0	0	0	0	0
Dec 1997	8	0	0	0	0	0	0	0
Jan 1998	8	0	0	0	0	0	0	0
Feb 1998	8	0	0	0	0	0	0	0

Monostroma hariotii

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0	1.1 ± 1.11	18.3 ± 6.07	18.9 ± 6.31	5.0 ± 1.88	1.7 ± 1.14	0
Jan 1997	6	0	1.1 ± 1.11	0	1.1 ± 1.11	0.6 ± 0.56	0	0
Feb 1997	6	0	0	0.6 ± 0.56	0	0	0	0
Apr 1997	6	0	0.6 ± 0.56	0.6 ± 0.56	0	0	0	0.6 ± 0.56
May 1997	6	0	0	0	0	0	0	0
Oct 1997	8	Ice-foot	0	0	0	0	0	0
Nov 1997	8	0	0	0	0	0	0	0
Dec 1997	8	0	0	0	0	0	0	0
Jan 1998	8	0	0	0	0	0	0	0
Feb 1998	8	0	0	0	0	0	0	0

Porphyra endiviifolium

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0.5 ± 0.50	0	0	0	0	0	0
Jan 1997	6	0	0.5 ± 0.50	0	0	0	0	0
Feb 1997	6	0	0	0	0	0	0	0
Apr 1997	6	0	0	0	0	0	0	0
May 1997	6	0	0	0	0	0	0	0
Oct 1997	8	Ice-foot	0	0	0	0	0	0
Nov 1997	8	0	0	0	0	0	0	0
Dec 1997	8	0	0	0	0	0	0	0
Jan 1998	8	0	0	0	0	0	0	0
Feb 1998	8	0	0	0	0	0	0	0

Acrosiphonia arcta

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	0	0	0	0	0	0	0
Jan 1997	6	0	6.7 ± 1.91	2.2 ± 1.14	0	0	0	0
Feb 1997	6	0	6.0 ± 2.00	5.0 ± 1.80	0	0	0	0
Apr 1997	6	0	6.7 ± 1.91	1.7 ± 1.17	0	0	0	0
May 1997	6	0	0	0.5 ± 0.50	0	0	0	0
Oct 1997	8	Ice-foot	0	0	0	0	0	0
Nov 1997	8	0	0	0	0	0	0	0
Dec 1997	8	0	0	0	0	0	0	0
Jan 1998	8	0	0	0	0	0	0	0
Feb 1998	8	0	0	0	0	0	0	0

Filamentous algae and diatom film

Month	n	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Dec 1996	6	94.4 ± 2.53	66.7 ± 4.47	21.1 ± 6.00	5.0 ± 1.88	0	0	0
Jan 1997	6	87.2 ± 1.81	71.7 ± 2.82	73.9 ± 4.34	37.8 ± 7.54	0	0	0
Feb 1997	6	91.1 ± 2.94	87.2 ± 3.59	8.9 ± 4.36	0.6 ± 0.56	0	0	0
Apr 1997	6	22.8 ± 7.01	13.3 ± 3.22	10.6 ± 5.40	0	0	0	0
May 1997	6	0	0	0	0	0	0	0
Oct 1997	8	Ice-foot	25.3 ± 5.60	43.1 ± 5.65	56.6 ± 3.24	64.0 ± 5.90	51.8 ± 5.71	66.6 ± 3.74
Nov 1997	8	0	14.5 ± 5.43	35.5 ± 9.00	49.0 ± 4.56	14.0 ± 8.91	30.6 ± 7.54	15.3 ± 6.06
Dec 1997	8	0	0	0	0	0	0.3 ± 0.25	0.3 ± 0.25
Jan 1998	8	0	0	0	0	0	0	0.8 ± 0.54
Feb 1998	8	0	0	0	0	0	0.3 ± 0.25	0.3 ± 0.25

Tab. A-4. Mean number (± standard errors) of *Nacella concinna* (Chapter 3.3.2.2)

St.	December 1996		January 1997		February 1997		April 1997		May 1997		August 1997	
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE
1	8	0	8	0	8	0	8	0	8	0	8	0
2	8	0	8	0	8	0	8	8.0 ± 4.84	8	0	8	0
3	8	0	8	2.5 ± 1.99	8	18.5 ± 16.8	8	22.5 ± 7.93	8	0	8	0
4	8	0	8	20.0 ± 9.50	8	128.5 ± 49.5	8	68.0 ± 8.18	8	41.0 ± 13.9	8	0
5	8	4.5 ± 2.67	8	112.5 ± 24.1	8	43.5 ± 14.6	8	93.5 ± 15.1	8	12.5 ± 11.4	8	0
6	8	17.0 ± 9.49	8	24.5 ± 8.93	8	30.5 ± 9.44	8	42.5 ± 11.2	8	35.5 ± 13.3	8	6.0 ± 3.02
7	8	27.5 ± 8.23	8	97.0 ± 25.6	8	41.0 ± 14.9		nd	8	26.5 ± 14.6	8	23.5 ± 16.7
8	8	62.5 ± 17.0	8	40.0 ± 12.6		nd		nd	8	106.0 ± 27.9		nd

St.	October 1997		November 1997		December 1997		January 1998		February 1998		March 1998	
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE
1	8	0	32	0	32	0	32	0.6 ± 0.36	32	2.9 ± 0.85	32	2.0 ± 1.05
2	8	0	32	0	32	1.5 ± 0.82	32	20.4 ± 6.19	32	35.5 ± 7.05	8	29.0 ± 11.4
3	8	0	32	0	32	15.6 ± 7.22	32	59.1 ± 13.2	32	69.1 ± 8.69	8	36.5 ± 8.23
4	8	0	32	20.6 ± 5.20	32	27.0 ± 6.87	32	102.4 ± 18.9	32	63.9 ± 7.68	12	78.0 ± 11.8
5	8	0	32	25.8 ± 4.94	32	42.0 ± 11.6	32	55.6 ± 13.2	32	47.4 ± 8.40	32	57.3 ± 6.73
6	8	4.0 ± 3.46	32	20.8 ± 4.79	32	49.4 ± 10.7	32	59.0 ± 9.65	32	70.8 ± 9.43	16	65.0 ± 10.4
7	8	11.5 ± 9.43	32	42.0 ± 4.17	32	28.6 ± 6.77	32	29.6 ± 7.94	32	37.6 ± 6.59		nd
8		nd	32	55.3 ± 9.07	32	63.9 ± 14.4	32	49.4 ± 8.36	32	53.8 ± 7.22		nd

Appendix

Tab. A-5. Mean size with standard errors, minimal and maximal size (mm) of *Nacella concinna* (4.3.1 and 4.3.2)

December 1996

St.	males				females				immatures				Σ			
	n	Mean ± SE	min	max	n	Mean ± SE	min	max	n	Mean ± SE	min	max	n	Mean ± SE	min	max
1	0				0				0				0			
2	0				0				0				0			
3	0				0				0				0			
4	0				0				0				0			
5	0				0				0				0			
6	15	33.5 ±0.8	27.5	37.5	19	31.2 ±0.7	27.0	37.0	0				34	32.3 ±0.5	27.0	37.5
7	20	28.7 ±0.7	23.7	35.7	35	27.0 ±0.4	20.2	33.6	0				55	27.6 ±0.4	20.2	35.7
8	50	27.6 ±0.5	20.0	35.0	55	26.5 ±0.5	20.9	35.0	2	14.3 ±1.2	13.4	15.1	107	26.3 ±0.4	13.4	35.0
Σ	85	28.9 ±0.4	20.0	37.5	109	27.5 ±0.3	20.2	37.0	2	14.3 ±1.2	13.4	15.1	196	27.6 ±0.3	13.4	37.5

January 1997

St.	males				females				immatures				Σ			
	n	Mean ± SE	min	max	n	Mean ± SE	min	max	n	Mean ± SE	min	max	n	Mean ± SE	min	max
1	0				0				0				0			
2	0				0				0				0			
3	0				5	30.8 ±1.7	26.8	35.4	0				5	30.8 ±1.7	26.8	35.4
4	11	32.9 ±1.0	27.9	37.1	24	31.0 ±0.9	21.9	39.2	0				35	31.6 ±0.7	21.9	39.2
5	14	29.9 ±0.7	26.3	36.4	26	29.6 ±0.5	25.4	35.9	0				40	29.7 ±0.4	25.4	36.4
6	18	28.6 ±0.6	24.7	34.2	20	29.1 ±0.7	24.0	36.1	0				38	28.8 ±0.5	24.0	36.1
7	20	28.7 ±0.7	24.8	35.7	21	26.0 ±0.6	21.1	32.4	1	17.3 ±		0	42	27.1 ±0.5	17.3	35.7
8	19	26.5 ±0.8	21.0	33.6	23	25.6 ±0.6	20.3	30.6	0				42	26.0 ±0.5	20.3	33.6
Σ	82	28.9 ±0.4	21.0	37.1	119	28.4 ±0.4	20.3	39.2	1	17.3 ±		0	196	28.6 ±0.3	13.4	39.2

February 1997

St.	males				females				immatures				Σ			
	n	Mean ± SE	min	max	n	Mean ± SE	min	max	n	Mean ± SE	min	max	n	Mean ± SE	min	max
1	0				0				0				0			
2	0				0				0				0			
3	10	33.6 ±0.8	29.5	37.2	25	32.7 ±0.8	22.9	40.2	0				35	32.9 ±0.6	22.9	40.2
4	13	31.7 ±1.1	26.0	37.3	18	29.2 ±0.7	23.2	35.6	0				31	30.3 ±0.6	23.2	37.3
5	12	30.5 ±0.8	25.2	35.4	19	29.6 ±0.6	25.3	34.3	0				31	30.0 ±0.5	25.2	35.4
6	12	28.2 ±0.7	23.2	31.2	19	28.6 ±0.8	24.2	35.3	0				31	28.5 ±0.5	23.2	35.3
7	17	28.0 ±0.6	24.7	33.8	13	28.1 ±0.4	25.7	31.3	0				30	28.0 ±0.4	24.7	33.8
8						nd										
Σ	64	30.1 ±0.4	23.2	37.3	94	29.9 ±0.4	22.9	40.2	0				158	30.0 ±0.3	22.9	40.2

April 1997

St.	males				females				immatures				Σ			
	n	Mean ± SE	min	max	n	Mean ± SE	min	max	n	Mean ± SE	min	max	n	Mean ± SE	min	max
1	0				0				0				0			
2	9	32.7 ±1.0	27.6	37.4	20	31.9 ±0.6	26.4	35.8	0				29	32.2 ±0.5	26.4	37.4
3	7	34.7 ±1.2	30.0	38.7	23	31.9 ±0.6	27.1	37.2	0				30	32.6 ±0.5	27.1	38.7
4	16	29.7 ±1.0	24.9	39.0	18	30.5 ±0.7	25.7	38.9	0				34	30.1 ±0.6	24.9	39.0
5	11	29.6 ±0.7	25.6	32.6	21	29.5 ±0.9	24.0	41.9	0				32	29.5 ±0.6	24.0	41.9
6	12	30.2 ±0.8	26.4	36.0	21	29.9 ±0.7	23.4	35.8	0				33	30.0 ±0.5	23.4	36.0
7						nd										
8						nd										
Σ	55	30.9 ±0.5	24.9	39.0	103	30.8 ±0.3	23.4	41.9	0				158	30.8 ±0.3	23.4	41.9

May 1997

St.	n	males Mean ± SE	min	max	n	females Mean ± SE	min	max	n	immatures Mean ± SE	min	max	n	Σ Mean ± SE	min	max
1	0				0				0				0			
2	0				0				0				0			
3	0				0				0				0			
4	12	33.4 ± 1.2	25.7	41.2	17	31.3 ± 1.0	23.2	41.1	0				29	32.1 ± 0.8	23.2	41.2
5	15	32.2 ± 0.8	28.4	38.8	14	30.0 ± 1.0	25.3	37.4	0				29	31.1 ± 0.7	25.3	38.8
6	13	32.4 ± 1.1	23.8	38.8	17	30.4 ± 0.8	26.0	35.6	0				30	31.3 ± 0.7	23.8	38.8
7	12	30.6 ± 0.8	24.8	36.0	19	30.5 ± 0.8	25.8	40.0	0				31	30.5 ± 0.6	24.8	40.0
8	13	28.7 ± 0.9	22.6	35.1	17	28.4 ± 0.6	24.1	32.4	0				30	28.5 ± 0.5	22.6	35.1
Σ	65	31.5 ± 0.5	22.6	41.2	84	30.1 ± 0.4	23.2	41.1	0				149	30.7 ± 0.3	22.6	41.2

August 1997

St.	n	males Mean ± SE	min	max	n	females Mean ± SE	min	max	n	immatures Mean ± SE	min	max	n	Σ Mean ± SE	min	max
1	0				0				0				0			
2	0				0				0				0			
3	0				0				0				0			
4	0				0				0				0			
5	0				0				0				0			
6	9	34.3 ± 1.3	30.2	39.8	21	29.7 ± 0.7	24.8	35.2	0				30	31.0 ± 0.7	24.8	39.8
7	6	29.4 ± 1.5	26.2	36.1	21	28.6 ± 0.6	24.3	35.5	0				27	28.8 ± 0.6	24.3	36.1
8									nd							
Σ	15	32.3 ± 1.1	26.2	39.8	42	29.1 ± 0.5	24.3	35.5	0				57	30.0 ± 0.5	24.3	39.8

October 1997

St.	n	males Mean ± SE	min	max	n	females Mean ± SE	min	max	n	immatures Mean ± SE	min	max	n	Σ Mean ± SE	min	max
1	0				0				0				0			
2	0				0				0				0			
3	0				0				0				0			
4	0				0				0				0			
5	0				0				0				0			
6	11	31.0 ± 1.1	25.1	36.5	20	31.0 ± 0.7	23.8	35.1	0				31	31.0 ± 0.6	23.8	36.5
7	10	30.5 ± 1.1	25.4	35.5	23	31.0 ± 0.7	24.5	38.0	0				33	30.8 ± 0.6	24.5	38.0
8									nd							
Σ	21	30.8 ± 0.8	25.1	36.5	43	31.0 ± 0.5	23.8	38.0	0				64	30.9 ± 0.4	23.8	38.0

November 1997

St.	n	males Mean ± SE	min	max	n	females Mean ± SE	min	max	n	immatures Mean ± SE	min	max	n	Σ Mean ± SE	min	max
1	0				0				0				0			
2	0				0				0				0			
3	0				0				0				0			
4	16	34.0 ± 0.7	30.5	41.9	29	32.7 ± 0.6	29.2	42.6	0				45	33.2 ± 0.4	29.2	42.6
5	21	31.6 ± 0.8	24.9	38.5	50	31.0 ± 0.5	25.6	38.7	0				71	31.2 ± 0.4	24.9	38.7
6	19	32.4 ± 0.8	26.4	37.6	48	30.6 ± 0.4	25.8	37.0	0				67	31.1 ± 0.4	25.8	37.6
7	27	30.0 ± 0.7	19.4	35.7	57	29.1 ± 0.4	23.9	35.2	1	13.9 ±	0		85	29.2 ± 0.4	13.9	35.7
8	37	27.6 ± 0.6	19.3	34.5	33	26.7 ± 0.5	21.1	35.1	0				70	27.2 ± 0.4	19.3	35.1
Σ	120	30.5 ± 0.4	19.3	41.9	217	30.0 ± 0.2	21.1	42.6	1	13.9 ±	0		338	30.1 ± 0.2	13.9	42.6

December 1997

St.	males n	Mean ± SE	min	max	females n	Mean ± SE	min	max	immatures n	Mean ± SE	min	max	Σ n	Mean ± SE	min	max
1	0				0				0				0			
2	0				0				0				0			
3	36	32.1±0.5	27.0	39.8	35	30.9±0.5	24.3	37.4	0				71	31.5±0.4	24.3	39.8
4	20	31.4±0.9	25.2	39.4	36	31.0±0.4	25.5	35.5	0				56	31.1±0.4	25.2	39.4
5	29	30.1±0.5	26.7	36.5	56	29.7±0.4	24.1	38.0	0				85	29.8±0.3	24.1	38.0
6	69	28.8±0.4	23.6	35.1	97	28.6±0.3	23.2	38.0	0				166	28.7±0.2	23.2	38.0
7	47	28.0±0.5	20.1	37.9	41	27.9±0.4	22.8	35.1	1	12.2±	0		89	27.8±0.4	12.2	37.9
8	59	27.0±0.4	20.4	34.7	55	26.5±0.4	20.6	33.2	0				114	26.8±0.3	20.4	34.7
Σ	260	29.1±0.2	20.1	39.8	320	28.9±0.2	20.6	38.0	1	12.2±	0		581	28.9±0.1	12.2	39.8

January 1998

St.	males n	Mean ± SE	min	max	females n	Mean ± SE	min	max	immatures n	Mean ± SE	min	max	Σ n	Mean ± SE	min	max
1	0				0				0				0			
2	14	30.7±0.8	25.1	35.2	30	30.5±0.5	25.0	36.7	0				44	30.6±0.4	25.0	36.7
3	44	30.2±0.5	25.1	38.4	85	29.3±0.3	24.3	43.1	0				129	29.6±0.3	24.3	43.1
4	44	31.1±0.5	25.4	36.2	58	28.1±0.5	22.5	37.6	0				102	29.4±0.4	22.5	37.6
5	58	28.9±0.4	22.5	35.0	67	28.1±0.4	21.8	38.7	0				125	28.5±0.3	21.8	38.7
6	65	27.8±0.4	22.6	34.9	93	27.4±0.3	22.5	36.7	0				158	27.6±0.2	22.5	36.7
7	38	27.1±0.4	22.6	33.6	38	26.2±0.4	22.0	33.3	0				76	26.7±0.3	22.0	33.6
8	51	26.5±0.5	19.6	35.8	49	25.9±0.4	20.3	34.1	3	12.1±2.2	8.0	15.6	103	25.8±0.4	8.0	35.8
Σ	314	28.6±0.2	19.6	38.4	420	27.9±0.2	20.3	43.1	3	12.1±2.2	8.0	15.6	737	28.2±0.1	8.0	43.1

February 1998

St.	males n	Mean ± SE	min	max	females n	Mean ± SE	min	max	immatures n	Mean ± SE	min	max	Σ n	Mean ± SE	min	max
1	23	32.7±0.7	26.2	38.2	28	32.6±0.7	25.8	39.4	0				51	32.6±0.5	25.8	39.4
2	17	32.2±0.8	27.7	37.6	41	30.6±0.4	25.9	36.2	0				58	31.1±0.4	25.9	37.6
3	60	29.9±0.4	24.6	38.9	53	29.2±0.4	24.0	35.1	0				113	29.6±0.3	24.0	38.9
4	32	28.5±0.6	22.8	39.1	36	27.2±0.5	21.5	35.9	0				68	28.1±0.4	21.5	39.1
5	41	28.8±0.6	20.9	39.7	39	28.0±0.5	23.5	36.6	0				80	28.4±0.4	20.9	39.7
6	47	28.4±0.5	19.8	37.6	59	27.8±0.4	22.8	35.8	0				106	28.1±0.3	19.8	37.6
7	53	28.1±0.4	23.3	36.0	58	26.5±0.3	21.9	32.1	0				111	27.3±0.3	21.9	36.0
8	52	26.4±0.4	20.9	33.8	51	25.7±0.4	20.4	34.9	0				103	31.0±0.3	20.4	34.9
Σ	325	28.9±0.2	19.8	39.7	365	28.2±0.2	20.4	39.4	0				690	28.5±0.1	19.8	39.7

March 1998

St.	males n	Mean ± SE	min	max	females n	Mean ± SE	min	max	immatures n	Mean ± SE	min	max	Σ n	Mean ± SE	min	max
1	6	32.5±1.4	26.5	37.0	10	31.3±0.8	25.9	35.1	0				16	31.7±0.7	25.9	37.0
2	25	31.9±0.7	26.4	40.5	33	31.5±0.6	23.9	37.5	0				58	31.7±0.4	23.9	40.5
3	35	30.6±0.5	24.3	36.6	38	29.5±0.5	23.0	38.7	0				73	30.0±0.4	23.0	48.7
4	23	28.4±0.6	23.0	36.6	30	28.5±0.7	24.0	40.0	0				53	28.5±0.5	23.0	40.0
5	33	27.9±0.4	23.4	33.8	23	27.8±0.5	24.0	33.8	0				56	27.6±0.4	23.4	33.8
6	28	29.6±0.6	22.5	34.4	24	27.8±0.5	23.4	35.2	0				53	28.8±0.4	16.1	35.2
7	27	26.9±0.5	20.8	34.0	25	26.6±0.5	22.8	33.8	1	16.1±	0		52	26.8±0.4	20.8	34.0
8	26	26.7±0.6	21.0	31.0	27	24.6±0.5	21.0	31.5	0				53	25.6±0.4	21.0	31.5
Σ	203	29.0±0.2	20.8	40.5	210	28.4±0.3	21.0	40.0	1	16.1±	0		414	28.7±0.2	16.1	40.5

Tab. A-6. Movement of *Nacella concinna* (Chapter 4.3.4)

y = vertical distance moved (cm) a day (negative value is straight down the beach). d = total distance moved (cm) a day.

26. 03. - 06. 04. 1997

| | Zone 1 | | | | | |
| | Large limpets | | Small limpets | | Sub-littoral limpets | |
	y	d	y	d	y	d
Count	18		19		18	
Mean	-17.5	23.0	-17.5	27.0	-52.2	60.8
SE	4.0	3.4	4.7	4.4	7.4	7.0
Min	-65.3	9.8	-71.0	6.1	-93.4	4.2
Max	-0.9	70.6	16.4	72.8	3.3	98.5

29. 11. - 12. 12. 1997

| | Zone 1 | | | | Zone 2 | | | |
| | Large limpets | | Small limpets | | Large limpets | | Small limpets | |
	y	d	y	d	y	d	y	d
Count	22		21		18		23	
Mean	7.7	18.3	-10.9	13.7	29.6	42.4	6.5	18.5
SE	6.4	5.8	2.9	2.8	9.8	10.2	5.2	4.4
Min	-19.8	0.5	-46.4	0.4	-20.3	1.4	-36.1	1.1
Max	95.4	95.4	5.2	46.5	140.2	177.6	74.1	75.2

16. 01. - 28. 01. 1998

| | Zone 1 | | | | Zone 2 | | | |
| | Large limpets | | Small limpets | | Large limpets | | Small limpets | |
	y	d	y	d	y	d	y	d
Count	24		23		29		22	
Mean	-11.8	35.2	-15.3	23.3	5.4	21.3	1.9	17.9
SE	4.9	3.8	3.5	4.5	4.3	4.6	3.5	5.3
Min	-52.7	2.9	-45.9	0.5	-28.1	1.0	-24.2	1.0
Max	47.4	74.5	9.5	84.7	92.3	109.5	43.3	114.2

Tab. A-7. Regression of gonad, somatic and total tissue weight on shell length of *Nacella concinna* (Chapter 5.3.2)

W, dry tissue weight (mg); L, shell length (mm).

Males

Month	n	Gonad mass Regression	r^2	somatic mass Regression	r^2	total tissue Regression	r^2
December 1996	81	$\log_{10}W = 2.626 \log_{10}L - 1.836$	0.438	$\log_{10}W = 2.924 \log_{10}L - 1.826$	0.838	$\log_{10}W = 2.880 \log_{10}L - 1.625$	0.791
January 1997	81	$\log_{10}W = 3.884 \log_{10}L - 3.570$	0.795	$\log_{10}W = 3.333 \log_{10}L - 2.381$	0.859	$\log_{10}W = 3.488 \log_{10}L - 2.455$	0.885
February 1997	64	$\log_{10}W = 3.263 \log_{10}L - 3.024$	0.447	$\log_{10}W = 3.212 \log_{10}L - 2.198$	0.891	$\log_{10}W = 3.194 \log_{10}L - 2.095$	0.875
April 1997	55	$\log_{10}W = 4.147 \log_{10}L - 4.300$	0.850	$\log_{10}W = 3.290 \log_{10}L - 2.307$	0.885	$\log_{10}W = 3.430 \log_{10}L - 2.439$	0.901
May 1997	64	$\log_{10}W = 3.910 \log_{10}L - 3.829$	0.700	$\log_{10}W = 3.387 \log_{10}L - 2.528$	0.882	$\log_{10}W = 3.513 \log_{10}L - 2.599$	0.876
August 1997	27	$\log_{10}W = 2.307 \log_{10}L - 1.377$	0.363	$\log_{10}W = 2.872 \log_{10}L - 1.833$	0.789	$\log_{10}W = 2.705 \log_{10}L - 1.431$	0.704
October 1997	43	$\log_{10}W = 3.936 \log_{10}L - 3.803$	0.645	$\log_{10}W = 2.867 \log_{10}L - 1.834$	0.906	$\log_{10}W = 3.163 \log_{10}L - 2.118$	0.861
November 1997	115	$\log_{10}W = 3.265 \log_{10}L - 2.752$	0.656	$\log_{10}W = 2.985 \log_{10}L - 1.965$	0.899	$\log_{10}W = 3.078 \log_{10}L - 1.947$	0.879
December 1997	253	$\log_{10}W = 3.374 \log_{10}L - 2.898$	0.578	$\log_{10}W = 2.759 \log_{10}L - 1.692$	0.826	$\log_{10}W = 2.976 \log_{10}L - 1.833$	0.789
January 1998	304	$\log_{10}W = 3.767 \log_{10}L - 3.452$	0.670	$\log_{10}W = 2.752 \log_{10}L - 1.645$	0.877	$\log_{10}W = 3.079 \log_{10}L - 1.950$	0.862
February 1998	316	$\log_{10}W = 3.742 \log_{10}L - 3.476$	0.357	$\log_{10}W = 2.909 \log_{10}L - 1.858$	0.884	$\log_{10}W = 3.154 \log_{10}L - 2.059$	0.807
March 1998	196	$\log_{10}W = 3.584 \log_{10}L - 3.234$	0.346	$\log_{10}W = 2.551 \log_{10}L - 1.341$	0.819	$\log_{10}W = 2.876 \log_{10}L - 1.654$	0.746
Combined all months						$\log_{10}W = 3.173 \log_{10}L - 1.958$	0.808

Females

Month	n	Gonad mass Regression	r^2	somatic mass Regression	r^2	total tissue Regression	r^2
December 1996	103	$\log_{10}W = 3.240 \log_{10}L - 2.706$	0.598	$\log_{10}W = 2.940 \log_{10}L - 1.828$	0.797	$\log_{10}W = 3.032 \log_{10}L - 1.823$	0.816
January 1997	113	$\log_{10}W = 3.345 \log_{10}L - 2.757$	0.644	$\log_{10}W = 3.223 \log_{10}L - 2.203$	0.877	$\log_{10}W = 3.296 \log_{10}L - 2.154$	0.876
February 1997	93	$\log_{10}W = 3.450 \log_{10}L - 3.370$	0.284	$\log_{10}W = 3.192 \log_{10}L - 2.151$	0.828	$\log_{10}W = 3.243 \log_{10}L - 2.157$	0.803
April 1997	103	$\log_{10}W = 4.245 \log_{10}L - 4.554$	0.701	$\log_{10}W = 3.263 \log_{10}L - 2.244$	0.898	$\log_{10}W = 3.386 \log_{10}L - 2.369$	0.893
May 1997	84	$\log_{10}W = 4.478 \log_{10}L - 4.712$	0.619	$\log_{10}W = 3.545 \log_{10}L - 2.725$	0.876	$\log_{10}W = 3.725 \log_{10}L - 2.893$	0.856
August 1997	69	$\log_{10}W = 3.981 \log_{10}L - 3.900$	0.424	$\log_{10}W = 2.856 \log_{10}L - 1.803$	0.815	$\log_{10}W = 3.168 \log_{10}L - 2.122$	0.744
October 1997	76	$\log_{10}W = 4.456 \log_{10}L - 4.636$	0.540	$\log_{10}W = 2.921 \log_{10}L - 1.908$	0.846	$\log_{10}W = 3.261 \log_{10}L - 2.272$	0.811
November 1997	212	$\log_{10}W = 4.272 \log_{10}L - 4.241$	0.716	$\log_{10}W = 3.086 \log_{10}L - 2.077$	0.893	$\log_{10}W = 3.414 \log_{10}L - 2.416$	0.882
December 1997	316	$\log_{10}W = 4.080 \log_{10}L - 3.928$	0.623	$\log_{10}W = 2.719 \log_{10}L - 1.622$	0.831	$\log_{10}W = 3.165 \log_{10}L - 2.098$	0.813
January 1998	404	$\log_{10}W = 4.113 \log_{10}L - 3.948$	0.669	$\log_{10}W = 2.730 \log_{10}L - 1.611$	0.838	$\log_{10}W = 3.198 \log_{10}L - 2.118$	0.856
February 1998	351	$\log_{10}W = 4.315 \log_{10}L - 4.281$	0.385	$\log_{10}W = 2.775 \log_{10}L - 1.652$	0.847	$\log_{10}W = 3.220 \log_{10}L - 2.136$	0.792
March 1998	199	$\log_{10}W = 3.352 \log_{10}L - 2.924$	0.210	$\log_{10}W = 2.461 \log_{10}L - 1.211$	0.796	$\log_{10}W = 2.765 \log_{10}L - 1.494$	0.694
Combined all months						$\log_{10}W = 3.127 \log_{10}L - 2.012$	0.799
Combined all data						$\log_{10}W = 3.085 \log_{10}L - 1.958$	0.808

Acknowledgements

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