# 平成 18 年度厚岸湖・別寒辺牛湿原学術研究奨励補助研究
# 調査報告書

## 海草藻場における一次消費者の群集構造の変動様式の解明と それに対する魚類群集の応答

千葉大学自然科学研究科
山田勝雅
kyamada@graduate.chiba-u.jp

### 【はじめに】

海草藻場は非常に豊富でしかも多様な生物群集を形成し、大型植物（海藻、海草）のみならず、藍藻、珪藻などの微小藻類、原生動物から脊椎動物にいたるまで、海産の殆どすべての動物門に属する動物が出現することが知られる (向井 1993, 相生 1996, 2000, 松政と向井 1996, Zouhiri *et al.* 1998, 大森 2000, 澤村 2000, 渡辺と仲岡 2000)。また、わが国においては水産資源の産卵場や育成場、水質浄化としての価値が古くから知られている (向井 1993, 相生 1996, 2000)。しかしながら近年の埋め立てをはじめ、陸から流入してくる雑排水による水質汚染などが原因で、草原のようであった大規模な群落は衰退し、現在はパッチ状の小規模な海藻群落になってしまっているものも少なくない (向井 1996, 仲岡 2000)。海草藻場に生息する生物の生態的な知見の蓄積は、そこに形成されている生態系の構造と機能を評価する上で不可欠であり、特に海草藻場の衰退が危惧される今日においては急務であると考えられる。

北海道厚岸湖内には海草藻場が広い範囲にわたって形成されている。厚岸湖において周年にわたり行われた曳網調査によって採集された試料より 20 属 38 種の端脚類 (Amphipoda)、7 属 9 種のアミ類 (Mysidacea)、5 属 5 種のクマ類 (Cumacea)、5 属 5 種の等脚類 (Isopoda)、4 属の十脚類 (Decapoda)、4 属の橈脚類 (Copepoda)をはじめ介形類 (Ostracoda)、毛顎動物 (Chaetognatha)、腹足類 (Gastropoda)、刺胞動物 (Cnidaria)、線形動物 (Nemathelminthes)、貧毛類 (Oligochaeta)、多毛類 (Polychaeta)、魚類 (Pisces) などが同定され、厚岸湖で多様な生物相が形成されていることが示されている (Vallet ら 未発表)。なかでも、採集された総個体数に対しアミ類が 77.2%を占めている (Yamada et al., 2007)。アミ類は植物から動物プランクトン、あるいはデトライタスにいたる多彩な餌を摂餌して成長・増殖する雑食性動物であると認識される (Mauchline 1980)。なかでも閉鎖水域においては、アミによる捕食がプランクトンの群集構造に影響を及ぼすことが指摘されている (e.g. Murtaugh 1981, Siegfried 1982, Wooldridge and Webb 1988, Hanazato 1990, Chigbu and Sibley 1994, Aaser *et al.* 1995)。

これらアミ類は北海道厚岸湖において、コマイ (*Eliginus grocilis*)、ハタハタ (*Arctoscopus* *japonicus*)、エゾアイナメ (*Hexagrammos steller*)、イソバテング (*Blepsias cirrhosus*)、ガジ (*Opisthocentrus cellatus*)などさまざまな魚類の主要な餌料となっており、湖内に出現する32種類の魚類の胃内容物には、アミ類が平均重量で 43％を占めていることが報告されている (Watanabe et al., 1995)。平成16年度厚岸湖・別寒辺牛湿原学術研究奨励補助制度の一環として行われた厚岸湖の全生物相の調査から (山田, 2005: 平成16年度学術研究奨励補助研究報告書)、厚岸湖内に生息する100mm以上に成長する比較的大型の魚類のなかで、シモフリカジカ *Myoxocephalus brandti* (Steindachner, 1867)、ムロランギンポ *Pholidapus dybowskii* (Steindachner, 1880)、タケギンポ *Pholis crassispina* (Temminck and Schlegel, 1845)の3種が湖内の大型魚類の9割以上を占めていたことが報告されている (山田 2006)。

シモフリカジカは漁業対象魚種として知られ、日本近海では、北海道の沿岸域の岩場や藻場に生息しており、体長35cmほどに成長することが知られる (渡辺ら, 1996)。一方で、ムロランギンポ、タケギンポは漁業対象種ではなく、藻場（海草場）においてしばしば採集されることが報告されており、ハビタットである海草と密接な関係 (association)を有していることが知られる。渡辺ら (1996) はこれら3種を含める厚岸湖に出現する魚類すべての胃内容物調査を行い、食性によって6グループに分類されることを示唆している。一方で、一般的に魚類は成長にともない食性を変化させることが知られ、5cm程度の大きさであれば、種にかかわりなく類似した食性を示すことも報告されている（体長・gape size依存型の捕食様式）(渡辺ら, 1996)。

厚岸湖において、餌である一次消費者と魚類は季節、場所によって劇的に変化する (例えば, 山田, 2005: 平成16年度学術研究奨励補助研究報告書, 堀ら 2005, 山田ら 2005, Yamada et al., 2007)。一次消費者であれば、季節的な水温変化に依存した再生産周期の違いによって各種の生物量が変化すると共に (山田 2006, Yamada et al., 2007)、別寒辺牛川から淡水が流入する河口から真龍へと続くに環境要因の著しい変化（勾配）は生物相に変化をもたらすだろう。これら一次消費者の種組成、生物量の時空間変動にともなって、一次消費者を餌とする魚種の分布や生物量も変化すると考えられる。さらに厚岸湖内に繁茂するハビタットとしての海草の有無も生息場所の変化に影響を与えることが予想される。これら複合的な生物的・非生物的要因を解明するためには、一次消費者の生物相の定量的な調査、魚種の各成長段階での食性の解明など、基礎的な知見を蓄積させ、段階的に評価する必要がある。

本報告書では特に、厚岸湖に優占する魚類3種、シモフリカジカ、ムロランギンポ、タケギンポの定量採集の結果と、成長段階（体サイズ）にともなう食性の変化について報告する。また、餌である一次消費者動物群集の時空間的変動および海草場の存在が優占する3種の生物量や生息域の変化に与える影響について考察する。なお、餌である一次消費者動物群集の時空間的変動様式については (山田, 2005: 平成16年度学術研究奨励補助研究報告書)、報告書末尾に添付する別紙を参照とする (英文 : 以下 Yamada et al., submittedとして引用)。

【材料と方法】

採集は、厚岸湖内 4 定点および湖外の 2 定点において (Yamada et al., submitted 参照)、2006 年 7 月〜12007 年 3 月に不定期に行われた。採集は高さ 40 ㎝、幅 50 ㎝、網目幅 500µm のそりネットを用いた。ネットの曳網時間は 3 分とし、 GPS（Global positioning system）によって記録されたネットの投入、揚収地点から曳網距離を求めた。

得られた試料、および 2004-2005 に採集された試料から、優占種 3 種を同定、計数し、各個体の体サイズを測定した。サイズクラス頻度分布を作成後、各サイズクラスからランダムに個体を選出し、胃内容調査に用いた。

胃内容物の充填度は目視によって 1-10 段階で評価した。出現した一次消費者は、同定、計数を行った後、各種について point method を用いての胃内容物に占める貢献度 [Volume 基準 (%)]の評価を行った (Hynes, 1950; Hyslop, 1980)。また、胃内容にみられた各個体については体サイズを測定した。魚類の消化により破損した甲殻類の個体の全長を測定するには、以下の回帰式を使用した (Yamada et al., unpublished)。

*Heptacarpus grebnitzkii*: $TBL = 2.760\ CL + 8.921$ ($R^2 = 0.8056$, $N = 61$)
*Pandalopsis pacifica*: $TBL = 2.962\ CL + 13.293$ ($R^2 = 0.8680$, $N = 113$)
*Crangon* sp.: $TBL = 4.095\ CL + 4.798$ ($R^2 = 0.9654$, $N = 42$),
*Acanthomysis shrenckii*: $Telson\ L = 0.163\ TBL + 0.0556$ ($R^2 = 0.6531$, $N = 117$)

ここで、TBL は全長、CL は背甲長、TL は尾節長を示している。この回帰式により、摂餌された際の餌個体の体長の評価が可能になる。

また、室内実験において、アミ類、その他の甲殻類の被食率の実験を行った。しかし、実験が未完了のため、本報告書では割愛する。

【結果と考察】

1. 優占種 3 種ともに、体サイズと共に餌サイズの幅が増加する傾向が見られた (Fig. 1)
2. 3 種の摂餌する餌サイズと体サイズの関係を比較したところ、3 種は成長に伴い異なる餌サイズを摂餌している傾向が見られた (Fig. 2)。このことは 3 種が厚岸湖内で共存できる理由のひとつかもしれない。
3. 体長に対する餌サイズの割合の変動は、3 種間で異なっていた (Fig. 3)。このことは、3 種の摂餌戦略が異なっていることを示唆している。具体的には
    ① シモフリカジカ：体サイズと共に餌サイズは一定になった (Fig. 3a)。このことは、成熟とともに大型の餌のみを獲得し、効率的に摂餌を行っていることが示唆される。
    ② ムロランギンポ：体サイズと共に餌サイズの幅は増加する (Fig. 3b)。このことは、成熟とともに摂餌可能な餌サイズの幅が増加し、様々なサイズや種を摂餌すること

    で効率的に摂餌を行っていることが示唆される。
    ③ タケギンポ：体サイズと共に餌サイズに変化は見られなかった (Fig. 3c)。このことは、タケギンポが高い餌獲得能力や戦略を有していることを示している。
    ④ ①～③のように摂餌戦略が異なることで3種の共存が可能となっているのかもしれない。

4. シモフリカジカが体長の約 5%の大きさの餌を摂餌するのに対し、ムロランギンポ、タケギンポは約 2%の大きさの餌を摂餌していた (Fig. 4)。このことは、gape サイズによって餌サイズの幅が決定されていることが示唆され、餌サイズの食べ分けを行うメカニズムのひとつと考えられる。
5. 春、幼魚の出現頻度がもっとも高かった (Fig. 5)。このことは、3 種にとって、春厚岸湖の特に河口域の海草場が幼魚の育成場として利用されていることを示唆している。
6. 分類群で見ると、3 種はサイズ変化に伴って食性を変化させていた (Fig. 5)。けれども、その変化に規則性は見られなかった。
7. Yamada et al., (submitted)をもとに、一次消費者を生息場基準で分類した機能群に分類したところ、体サイズに伴って摂餌する機能群が変化する傾向が見られた (Fig. 6)。このことは 3 種が餌グループを食い分けをしていることを示唆している。
8. 体長と共に変化する機能群の割合についてロジット回帰を行った結果3種は異なる傾向を示した (Fig. 7)。具体的には
    ① シモフリカジカ：体サイズと共に、エビ類、魚類を摂餌する割合が増加する。
    ② ムロランギンポ：小型サイズ時にはカイアシ類や小型のアミ類を摂餌しているが成長に伴い、海草の葉の表面に定着するヨコエビ類や等脚類を摂餌するようになる。けれども、アミ類はどの体サイズにおいても重要な餌料となっている。
    ③ タケギンポ：小型サイズ時には小型のアミ類を摂餌するが、成長に伴い、海草の葉の表面に定着するヨコエビ類、ワレカラ類、等脚類を摂餌するようになり、成体になると殆どアミ類を摂餌しない。
    ④ ①～③は 3 種が餌種を食べ分ける共存機構と考えられる。
9. 各定点において採集された 3 種の胃内容物組成 (V%の平均値)の変化から、タケギンポは海草の有無によって食性が著しくことなる一方で、シモフリカジカとムロランギンポには著しい変化は見られなかった。このことは、特にタケギンポは海草との association が強いことで餌種を食べ分けていることが示唆される (Fig. 8)。

厚岸湖における一次消費者動物群集は、季節的に有意に生物相（多様性・生物量・種組成）が変化すると共に、河口から海洋にかけての塩分勾配に伴って生物相が規則的に変化することが前回の報告書からさらに解析を進めた結果明らかになった (Yamada et al., submitted)。一方で魚類の胃内容物に同様の傾向は認められなかった。このことは、3 種の魚類が厚岸湖内外の移動を頻繁に行っていることを示唆しており、生活史を示すサイズ分

布図と矛盾しない (Fig. 5)。

以上のことから厚岸湖に優占する魚類 3 種は、移動、餌サイズの食べわけ、餌グループの食べ分けを効率的に行うことで 3 種は共存を果たしていることが示唆された。このことは逆に、3 種が厚岸湖に生息する一次消費者の各種の生物量をバランスよく間引きすることによって、海草、付着藻類、一次消費者、魚類という低次栄養段階から高次栄養段階への流れを円滑にし、厚岸湖生態系の維持に重要な役割を果たしていることが示唆される (長谷川 2006 も参照)。漁業活動によってカジカなどの種を過剰に漁獲すると、カジカが摂餌している一次消費者の種やグループが著しく増加すると考えられ、厚岸湖生態系が変化することは十分に考えられる。

今後、餌獲得をどのように行っているか、個体間が干渉するような状態になったとき、どのような要因で餌獲得種が決定されるかを室内実験によって解明することでより詳細な餌の食べ分けの機構が明らかになるだろう。

【引用文献】

Aaser, H. F., F. Jeppenson and M. Søndergaard (1995) Seasonal dynamics of the mysid *Neomysis integer* and its predation on the copepod *Eurytemora affinis* in a shallow hypertrophic brackish lake. *Marine Ecology Progress Series,* 127: 45-56.

相生啓子 (1996) 藻場生態系 －アマモ場を中心に－. 遺伝, 50 (7)**:** 24-29.

相生啓子 (2000) アマモ場研究の夜明け. 海洋と生物, 22(6): 516-523.

Chigbu, P and T. H. Sibley (1994) Predation by *Neomysis mercedis*: effects of temperature, *Daphnia magna* size and prey density on ingestion rate and size selectivity. *Freshwater Biology,* 32: 39-48.

Hanazato T. (1990) A comparison between predation effects on zooplankton communities by *Neomysis* and *Chapborus. Hydrobiologia,* 198: 33-40.

Hasegawa, N., 2006. Studies on biological interactions and seagrass functions in a seagrass ecosystem. Ph.D. Thesis,

堀 正和, 長谷川夏樹, 山田勝雅, 田中義幸. 厚岸湖海草藻場生物群集における機能群構造と生態系機能との関係. 2005 年日本プランクトン学会・日本ベントス学会合同大会. 2005 年 9 月. 厚岸. 同学会講演要旨集. p. 39.

松政正俊、向井 宏 (1996) 藻場(海中植物群落群）の生物群集（9）－葉上動物の競争と移動性－. 海洋と生物, 18(3):218-222.

Mauchline, J., 1980. The biology of mysids and euphausiids. Advances in Marine Biology 18: 1-681.

向井 宏 (1993) 藻場(海中植物群落群）の生物群集（1）－多様性を支える種間関係－. 海洋と生物, 5(6):394-396.

Murtaugh, P. A. (1981) Selective predation by *Neomysis mercedis* in Lake Washington. *Limnology and Oceanography,* 26 (3): 445-453.

仲岡雅裕 (2000) 海草の保全に向けた世界的な取り組み：地域規模および地球規模のネットワークの構築について. 海洋と生物, 22 (6): 556-569.

大森雄治 (2000) 日本の海草－分布と形態－. 海洋と生物, 22(6): 524-532.

澤村正幸 (2000) スガモ場における魚類・ベントス間の食物網構造. 海洋と生物, 22 (6): 542-549.

Siegfried, C. A. (1982) Trophic relation of *Crangon franciscorum* Stimpson and *Palaemon macrodactylus* (Rathbun): Predation on the opossum shrimp, *Neomysis mercedis* (Holmes). *Hydrobiologia*, 89: 129-139.

渡辺研一、南 卓志、飯泉 仁、今村茂生 (1996) 北海道厚岸湖における魚類の胃内容物から見た種間関係. 北海道区水産研究所報告, 60**:** 239-276.

渡辺雅子、仲岡雅裕 (2000) 海草の分布と生産に影響を与える環境要因・生物学的要因. 海洋と生物, 22(6): 533-541.

Wooldridge, T. H. and P. Webb (1988) Predator-prey interactions between two species of estuarine mysid shrimps. *Marine Ecology Progress series,* 50: 21-28.

Yamada, K., K. Takahashi, C. Vallet, S. Taguchi & T. Toda, 2007. Distribution, life history and production of three species of *Neomysis* in Akkeshi-ko estuary, northern Japan. Marine Biology 150: 905-917.

山田勝雅, 堀 正和, 田中義幸, 長谷川夏樹, 仲岡雅裕. Effect of predation to size distribution of macrofaunal assemblage in seagrass bed, northern Japan. 第53回日本生態学会. 2006年3月. 新潟. 同学会講演要旨集. p. 267.

山田勝雅, 堀 正和, 田中義幸, 長谷川夏樹, 仲岡雅裕. 河口域から沿岸域における海草藻場の一次消費者の分布様式と海草・付着藻類との相互作用. 2005年日本プランクトン学会・日本ベントス学会合同大会. 2005年9月. 厚岸. 同学会講演要旨集. p. 42.

Zouhiri, S., C. Vallet and P. Mouny (1998) Spatial distribution and biological rhythms of suprabenthic mysids from the English channel. *Journal of the Marine Biological Association of the United Kingdom,* 78: 1181-1202.

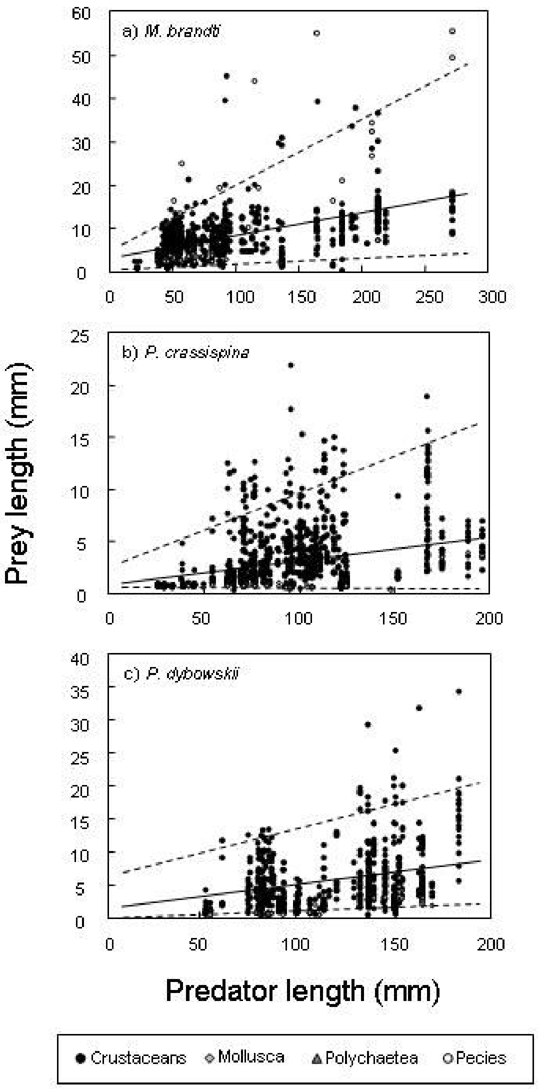

Fig. 1. Predator size - prey size scatter diagrams for three dominat predatory fishes in Akkeshi-ko estuary. Each symbol represents a single prey consumed by a predator. Regression lines indicate ontogenetic changes in prey size consumed with increasing predator size for all prey combined, dashed lines: minimum and maximum prey size, and continuous lines: mean prey sizes.

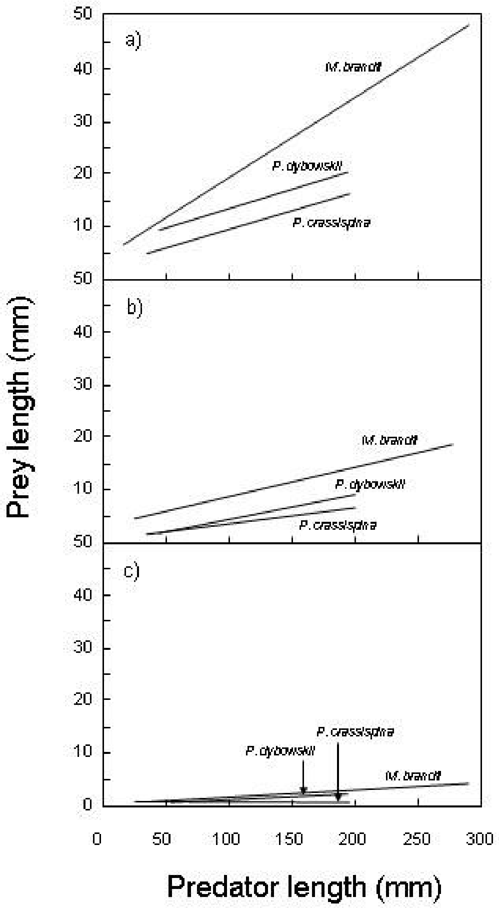

Fig. 2. Regressions illustrating ontogenetic changes in (a) maximum, (b) mean and (c) minimum prey size consumed with increasing predator size for three dominant fish predators examined in this study. Regressions equations are presented in Table ?. Each graph is intended to illustrate among-predator variation in prey size eaten.

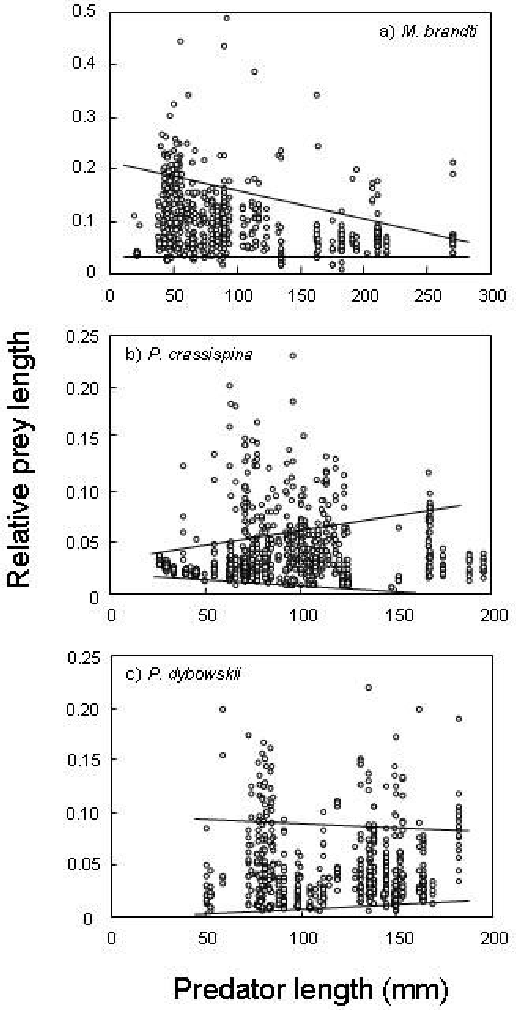

Fig. 3. Scatter diagrams illustrating relative prey size (prey size / predator size ratio) as a function of predator size. Each symbol represents a single prey consumed by a predator. Regression lines illustrate ontogenetic changes in the range of relative prey size consumed with increasing predator size. Regression slopes for upper (99th quantile) and lower (1st quantile) bounds are presented in Table ?.

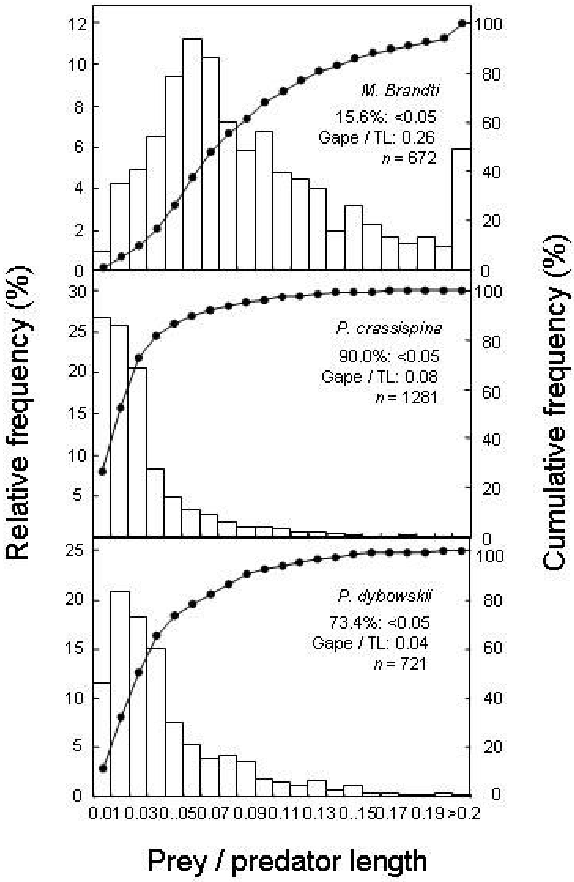

Fig. 4. Relative frequency distributions of prey size / predator size ratios consumed by three dominant fish predators in Akkeshi-ko estuary. For predators with gape information, average ratio of gape size to body size (Gape/TL) is indicated. *n* indicates number of individuals measured.

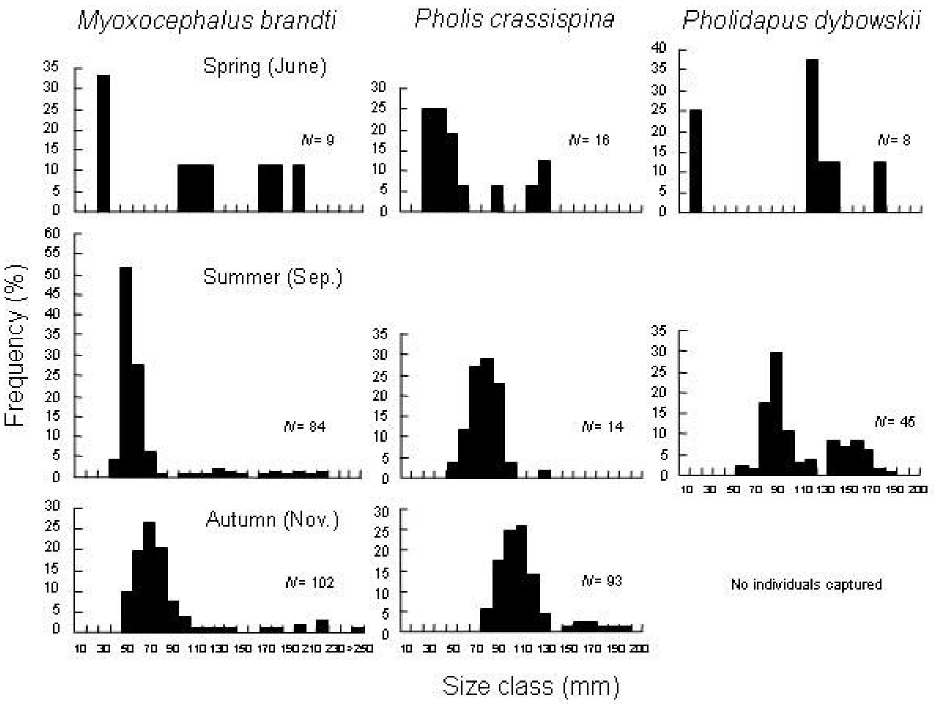

Fig. 5. Size frequency distributions of three fishes, *Myoxocephalus brandti, Pholis crassispina and Pholidapus dybowskii* at spring, summer and Autumn of 2006 in seagrass bed of Akkeshi-ko estuary. *n* indicates number of individuals measured for size.

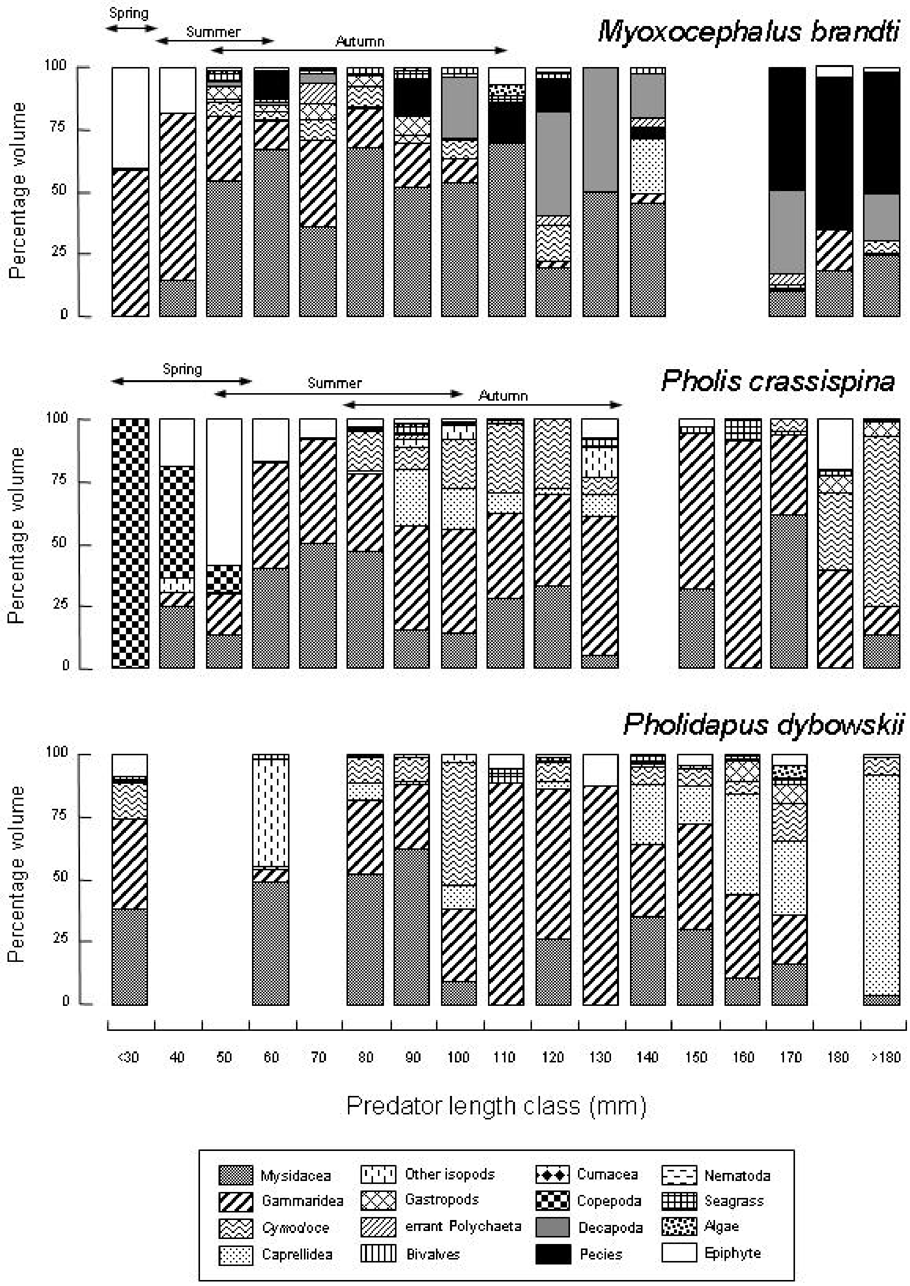

Fig.6. Stomach contents of three dominant fish species in Akkeshi-ko estuary. Prey organisms were classified into taxonomy.

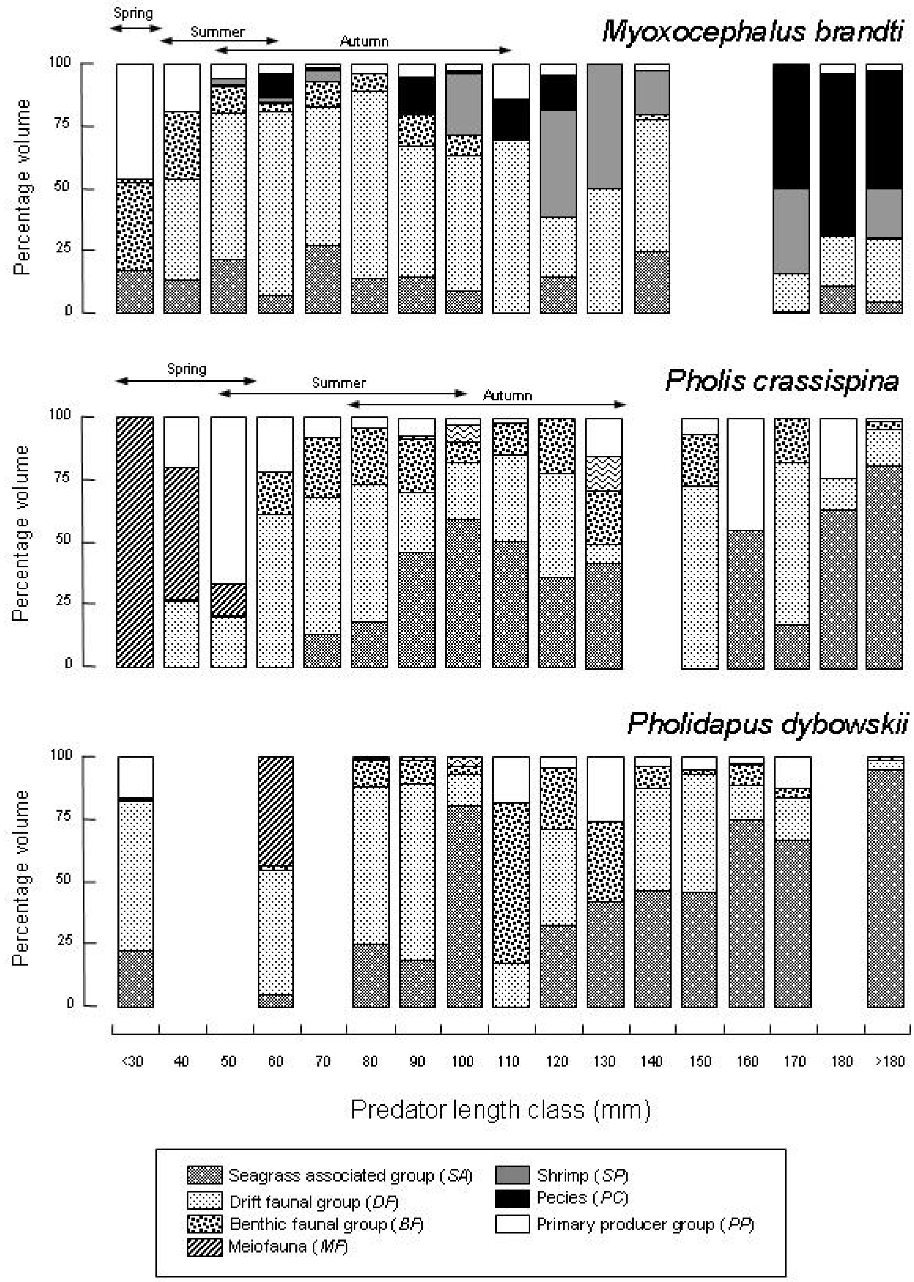

Fig.7. Stomach contents of three dominant fish species in Akkeshi-ko estuary. Prey organisms were classified into functional group.

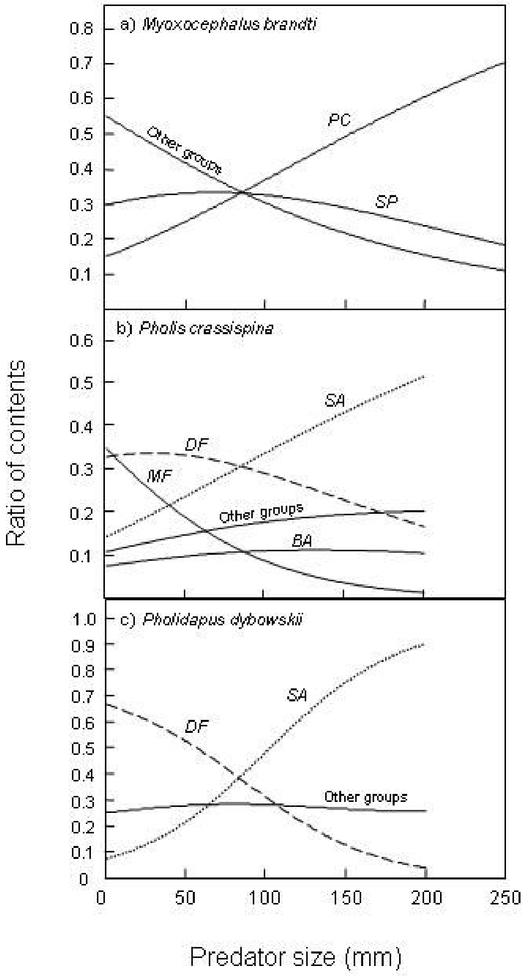

Fig.7. Variation of stomach contents with growth stage (body length) three dominant fish species in Akkeshi-ko estuary. Prey organisms were classified into functional group.

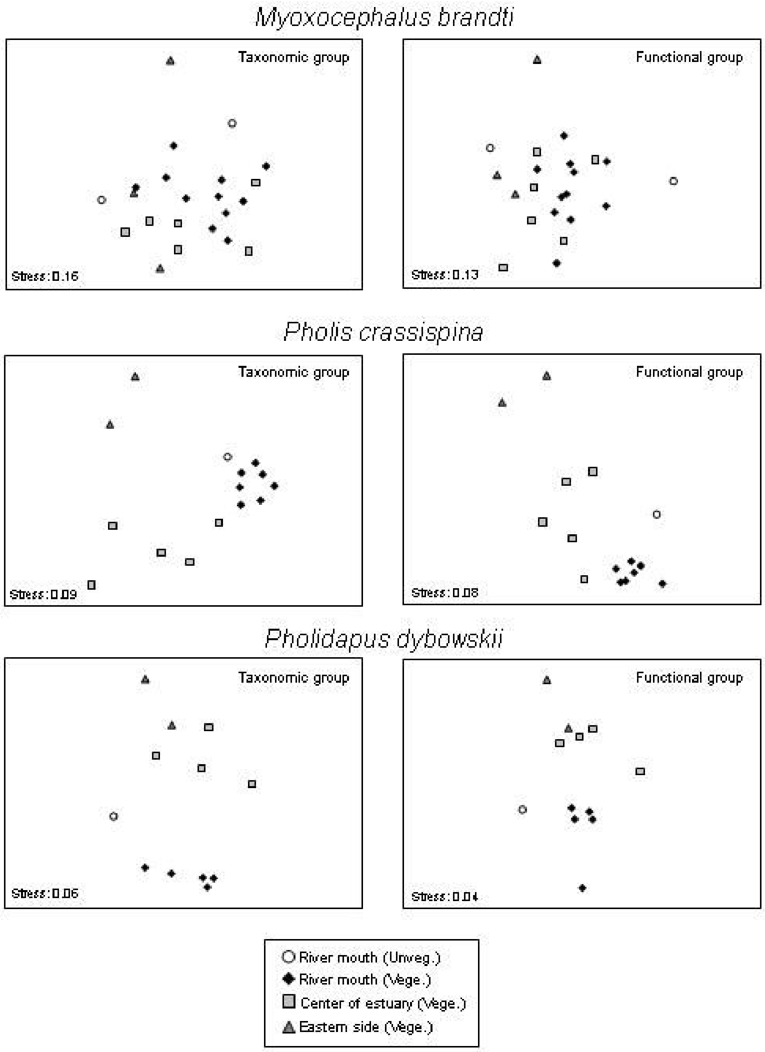

Fig. 8. Results of MDS plots showing similarity of community structure in stomach contents of three dominant fishes in different sites.

# 添付書類

# Yamada et al., submitted

# Temporal and spatial macrofaunal community changes along a salinity gradient in seagrass meadows of Akkeshi-ko estuary and Akkeshi Bay, northern Japan

Katsumasa YAMADA*

*Graduate School of Science and Technology, Chiba University, 1-33 Yayoi-cho, Inage, Chiba
263-8522, Japan

Tel.: +81-43-2903929, Fax: +81-43-2903929
*E-mail address*: kyamada@graduate.chiba-u.jp

**Keywords:** Macrofauna; Community structure; Salinity gradient; *Zostera* spp.; Northern Pacific coast.

## Abstract

Temporal and spatial variation of the macrofaunal community was investigated in seagrass meadows in Akkeshi-ko estuary and coastal area of Akkeshi Bay, northern Japan. We specifically addressed the question of how the salinity gradient in seagrass meadows affects the species richness, abundance and similarity of faunal groups classified based on the degree of association with the seagrasses, i.e. highly motile species that drift in the water column among seagrass blades (drift-fauna, *DF* group) and less motile species that are tightly associated with seagrass substrates (**s**eagrass-associated fauna, *SA* group). A total of 70 species were collected semi-quantitatively using an epibenthic sledge, among which more than one third of the species were captured in all areas, and a quarter of species only in the marine area. Significant spatial variation in species richness, as well as a positive relationship between salinity and species richness was found for most sampling occasions and for both functional groups. Whereas, relationship between salinity and abundance of macrofauna was not clear although significant time and site interactions were found for both functional groups. Patterns of similarity of assemblages varied between the functional groups: clear differences by sampling sites were discerned for *DF* group but not for *SA* group. These results provided evidence that the macrofaunal community structures in seagrass beds varied with the salinity gradient, but the pattern differed with time and between functional groups, possibly due to the effect of biotic and abiotic factors that also changed with salinity.

## Introduction

Seagrass generally enhances the faunal diversity by increasing habitat complexity, providing living space and shelter for a great variety of animal species (Lewis, 1987; Edgar et al., 1994; Jernakoff et al., 1996). However, the degree to which seagrass contributes to enhanced faunal abundance and diversity varies among sites and studies (Hemminga & Duarte, 2000). Numerous factors have been ascribed to be responsible for the observed variation in epifauna associated to seagrass beds, including abiotic factors such as salinity (Edgar & Barrett, 2002), depth (Gambi et al., 1992), periodic anoxia (Diaz & Rosenberg, 1995) and biotic factors such as species composition and morphological variation (Nakaoka et al., 2001) as well as competition and predator-prey interactions among animals (Orth et al., 1984; Edgar &

Aoki, 1993).

Seagrass beds develop in coastal areas of broad environmental gradients, and are often subjected to strong environmental fluctuations, especially of salinity. A temperate seagrass, *Zostera marina,* grows within a salinity range of 5-42 (van Katwijk et al., 1999). Salinity gradient, i.e. spatial variation in average and temporal fluctuation in salinity, has been thought to play an important role in determining the composition of the macrofaunal community in estuaries (e.g., Day, 1981; Williams et al., 1990; Smith & Witman, 1999). Lower salinity generally lead to less species diversity and higher individual abundance (e.g., Remane & Schlieper, 1971; Montagna & Kalke, 1992; Mannino & Montagna, 1997; Ysebaert et al., 1998; 2003). Most of these studies were conducted at unvegetated sand flat and mud bottom areas, whereas fewer studies have investigated the effects of salinity gradient on faunal community in seagrass meadows (Montague & Ley, 1993; Schlacher & Wooldridge, 1996; Edgar & Barrett, 2002).

Although a greater variety of benthic species inhabit seagrass meadows (Kikuchi, 1966; Hemminga & Duarte, 2000), their association degree with seagrass varies among species and taxonomic groups. For example, some amphipods such as *Caprella* spp. and *Ampithoe* spp. firmly attach to seagrass blades, whereas motile species such as mysids and shrimps mostly drift in the spaces between seagrass shoots and only occasionally attach to seagrass blades. The effect of salinity and other environmental variables within seagrass meadows may operate differently in the presence of a different macrofaunal association degree or motile ability, leading to a different community structure.

This study aims at examining temporal and spatial variations of the macrofaunal community along a salinity gradient in a seagrass meadow from the inner part of the estuary to the sea coast of Akkeshi-ko estuary and Akkeshi Bay, located on the eastern coast of Hokkaido, Japan. We examined how univariate and multivariate variables representing abundance, diversity and between-site similarity of macrofaunal community vary with different salinity levels. The patterns of variation were compared between species with different seagrass association degree, i.e. between highly motile species that mostly drift water column among seagrass blades (drift-fauna, *DF* group) and less motile species that are tightly associated with seagrass substrates (seagrass-associated fauna, *SA* group).

## Materials and Methods

### *Study area*

Akkeshi-ko estuary is located in the eastern part of Hokkaido, northern Japan (Fig. 1). It is connected to Akkeshi Bay by a narrow channel (*ca.* 500 m wide). The south of Akkeshi Bay is open to the Pacific Ocean. The surface area of the estuary and Akkeshi Bay is 32 and 110 km$^2$, respectively. Water depth in the most part of Akkeshi-ko estuary is between 0.8-1.7 m (Iizumi et al., 1995; Yamada et al., 2007), with a maximum of 10 m near the channel. Three rivers (Bekanbeushi, Tokitai and Tobai Rivers) flow into the estuary. Bekanbeushi River has the largest catchment area, accounting for 98.8 % of the total outfall to Akkeshi-ko estuary. Its average daily outfall accounting for 5.8 % of total volume of the Akkeshi-ko estuary (Iizumi et al., 1995). The flow input from Bekanbeushi River varied from 34 m$^3$ s$^{-1}$ (flood tide) to 42 m$^3$ s$^{-1}$ (ebb tide) in May and from 6 m$^3$ s$^{-1}$ to 13 m$^3$ s$^{-1}$ in October (Hasegawa, 2006).

A major part of Akkeshi-ko estuary is covered with two species of *Zostera* seagrasses; *Zostera marina* covers a wide range of subtidal area and *Z. japonica* occurs at the intertidal zones of the estuary, except for unvegetated bottoms near of the channel (deepest area in Akkeshi-ko estuary: mean 5.4 m, Yamada et al., 2007), the mouth of Bekanbeushi River flowing, and cultivation ground for clam (*Ruditapes* *philippinarum*) and oyster (*Crassostera gigas*) that occur scattered in shallow areas of Akkeshi-ko estuary (Kasim & Mukai, 2006).

Three seagrass species occur in Akkeshi Bay. *Zostera asiatica*, an endemic species to Japan and Korea, is dominant, occurring from the intertidal zone to the deepest edge (5 m below MLW) of the subtidal parts of seagrass bed (Watanabe et al., 2005). Distribution of *Z. marina* and the surfgrass *Phyllospadix iwatensis* is restricted to the shallower edge of the bed (intertidal zone to < 2 m deep); they occur in small patches on sandy and rocky substrata, respectively (Hamamoto & Mukai, 1999; Hasegawa et al., 2005; Watanabe et al., 2005; Sasil-Orbita & Mukai, 2006).

In the present study, six stations were established for the temporal collection of macrofauna. Stn. A was mainly covered by the muddy bottom (with a depth of 0.8 m) near the mouth of Bekanbeushi River. This station was unvegetated although a few patches of *Z. marina* (1-4 shoot/patch) have been observed occasionally (Yamada, K. & N. Hasegawa, personal observation). We nevertheless included this station in the present study because some motile species such as mysid and shrimp were observed to occur abundantly here (Yamada et al., 2007). Stns. B, C and D were located in *Z. marina* beds; near the river mouth (Stn. B, with the depth of 0.9 m), in the center (Stn. C, 1.5 m) and in the southern part of the estuary (Stn. D, 1.1 m). Stns. E and F were located in the seagrass beds at Akkeshi Bay, near the channel connecting the estuary and Akkeshi Bay (Stn. E, with the depth of 1.7 m) and along the northern coast at *ca.* 6 km in distance from the estuary (Stn. F, 2.0 m). The sites within Akkeshi-ko estuary (Stns. A-D) and Stn. E in Akkeshi Bay were the same as those described by Iizumi et al. (1995), Oshima et al. (1999), Hasegawa (2006) and Yamada et al. (2007); Stn. F by Hamamoto & Mukai (1999), Watanabe et al. (2005) and Sasil-Orbita & Mukai (2006).

Monthly mean aboveground biomass of *Z. marina* collected in the same period with this study varied between 28-135 g DW $m^{-2}$ at Stn. B, 75-242 g DW $m^{-2}$ at Stn. C and 99-200 g DW $m^{-2}$ at Stn. D (Hasegawa, 2006; Hasegawa et al., 2007). Monthly average biomass of *Z. marina* and *Z. asiatica* at Stn. F varied between 182-470 g DW $m^{-2}$ and 234-903 g DW $m^{-2}$, respectively (cf. Watanabe et al., 2005). Seagrass biomass at Stn. E was not measured quantitatively although the abundance of *Z. marina* and *Z. asiatica* was similar to that at Stn. F (Nakaoka, M., personal observation).

Salinity at the six stations was measured in June 2004, the same period with this study, at every 0.5 m above the bottom by T-S meter (ACT2-D, Alec. Elec. Co.). Such snapshot samplings of salinity may not represent actual salinity gradient of these sites because salinity is subject to change widely with tide and sporadic inflow of river water after heavy rain. We therefore collected previous data on salinity from all available sources that have been measured in June, September and November of 1993, 1997, 2001 and 2005 (Iizumi et al., 1995; Watanabe et al., 2005; Yamada et al., 2007; Tanaka et al., unpublished).

### *Sampling procedure*

The macrofauna sampling in the water column was carried out at three temporal terms in 2004 (spring: 8-12 June; summer: 2-6 September; autumn: 18-22 November) but not in winter because the estuary was covered by ice. In the study areas, at each sampling campaign, three replicates were collected using an epibenthic sledge (40 cm height, 60 cm width, 500 µm mesh). The sledge was towed horizontally for 40 m distance (*ca.* 3 min, 0.5-1.0 m $s^{-1}$). Actual distance of each tow was measured using a GPS plotter (JLU-128, JRC). Great care was paid when towing the sledge so that it did not overturn, and that the net was not clogged by seagrass leaves and other debris. Although the epibenthic sledge collects macrofauna with large amount of seagrass leaves it does not contain all seagrass in the towing area (cf. McNeill & Bell, 1992). Therefore, the macrofaunal sampling is not totally quantitative but rather regarded as semi-quantitative, with macrofaunal species associated tightly with seagrass (i.e., *SA* group) possibly underestimated.

On the whole, 54 samples were collected during the daytime at mid tide in order to minimize the effect of tidal flow. Samples were preserved in 10 % formalin seawater. In the laboratory, samples were washed and seagrass leaves were removed. They were then carefully washed again using 1 mm sieves to remove other debris. Thus, the abundance of macrofauna smaller than 1 mm in size may possibly be underestimated. Collected macrofauna was first classified to 6 taxonomic groups (shrimp, gastropod, amphipod, isopod, tanaid and mysid), and then to species. The number of individuals were counted for each species. Polychaetes were also captured in some samples although data of polychaetes were not used in the present study because they were not identified to species due to very small size (consisting only of juveniles).

*Macrofaunal grouping*

Identified macrofaunal species were categorized into two groups, drift-faunal group (*DF*) and seagrass-associated group (*SA*). *DF* consisted of highly motile species that mostly drift in the water column among seagrasses and rarely attached to seagrass blades, whereas *SA* is a group of epifauna firmly attached to seagrass substrates. The classification of each species to the two groups was carried out based on available information on behavior of each taxon. All mysid and shrimp species were classified to *DF* according to references (Mauchline, 1980; Miyake, 1982). Detailed information for behavior of each species occurred in this study area were referred also by Murano (1963), Zelickman (1974), Ohtsuka et al. (1995) and Yamada et al. (2007) for the mysids and Yamashita and Hayashi (1984), Mukai (1990), Komai (1999) and Tayasu et al. (1999) for the shrimps.

Almost all amphipod species were categorized according to Sawamura (2000) who investigated the microhabitat and feeding type of all faunal species captured in a surfgrass (*Phyllospadix iwatensis*) bed in western Hokkaido. Sawamura (2000) categorized gammarid species (*ca.* 100 species) into 11 groups (borer, commensal, epi-infaunal, epifaunal, infaunal, interstitial, pelagic, phreatic, periphytic, streams and terrestrial). In this study, 24 species of gammarid described by Sawamura (2000) were collected that belonged to the 11 groups. All species in the epi-infaunal, epifaunal and periphytic groups were first classified to *SA* group, except for some gammarid amphipods such as *Pontogeneia rostrata* and *Corophium* spp. that have been reported empirically less firmly attached to seagrass blades (e.g., Crawford, 1937; Pelegri et al., 1994; Yu et al., 1999; Saigusa et al., 2000). All caprellid species (9 species) categorized into periphytic groups by Sawamura (2000) were classified to *SA* group. The functional grouping of some species that were not described in Sawamura (2000) or identified to the species level (but genus level) was made by information on the congeneric species given in Sawamura (2000).

All isopod and tanaid species were classified into *SA* group referred by Mukai (1971), Oishi & Saigusa (1999), Saigusa et al. (2000), and Nakaoka (2003). Three gastropod species classified into *SA* group according to Toyohara et al. (1999) (for *Lirularia iridescens*) and Kanamori et al. (2004) (for *Lacuna decorata* and *L. uchidai*). For other species without literature information about association with seagrass blades (isopod: *Paranthura japonica* and *Idotea* sp., and gastropod: *Barleeia angustata*, *Temanella turrita*, *Batillaria multiformis*, *Reticunassa acutidentatus*, *R. fratercula hypolia*, *Retusa* sp. and *Margarites pilsbryi*), we examined their habitat requirement by observations in an indoor aquarium tank. Several leaves of *Z. marina* collected from Akkeshi-ko estuary were planted in a tank (13 l) with running seawater, and a number of >10 individuals of each species were added. Individual position (either on seagrass leaves or at other sites) was then observed with a hour frequency. In all examinations, individuals of each species revealed either of the two alternative behaviors; to stay exclusively on seagrass leaves or on other substrata. The former species was classified to *SA* group and the latter to *DF* group.

*Data analysis*

Spatial and temporal variation in species richness and abundance of total macrofauna and two groups of fauna (*SA* and *DF*) were compared by two-way ANOVA using sampling time and site as fixed factors. To reduce heterogeneous variance associated with positive correlation between mean and standard deviation, abundance data were log ($x$+1) transformed prior to the analysis. When a significant interaction between time and site was detected, multiple comparisons of means among sites was conducted for each time separately by Tukey's test using the mean square of residuals of the original two-way ANOVA (Day & Quinn, 1989; Quinn & Keough, 2002).

Spatial and temporal similarities on the whole macrofauna and between the two functional groups were graphically depicted using non-metric multi-dimensional scaling (MDS) and the ordination method (Clarke & Gorley, 2001; Clarke & Warwick, 2001) using the software PRIMER-E (ver. 5; Plymouth Marine Laboratory, UK). Abundance values and the presence/absence of each macrofaunal species were used, respectively. The similarity matrix obtained from the abundance values was calculated by the Bray-Curtis index with double square-root-transformed ($N^{1/4}$) data, as recommended by Faith et al. (1987) and Clarke (1993). To test temporal and spatial variation in assemblage structure, two-way analysis of similarities (ANOSIM; Clarke, 1993) was then undertaken using sampling time and site as factors (Clarke & Warwick, 2001).

Correlation between salinity matrix and similarity matrix was tested using the Mantel test for each season and for each functional group. Salinity matrices were constructed using the absolute difference in average salinity between a pair of stations as each element (i.e., $a_{ij} = \left|\bar{s}_i - \bar{s}_j\right|$, where $\bar{s}_i$ was the average salinity at site $i$). The Mantel test was carried out using the observed Pearson correlation coefficient as a test statistic against a permutation distribution generated by 720 iterations of data (exact permutation distribution for 6 × 6 matrices). The calculation was carried out using software 'zt' (Bonnet & Van de Peer, 2002).

## Results

*Variation in salinity*

Salinity observed at several occasions between 1993 and 2005 did not deviate greatly when compared for each station and season (Table 1). It was slightly higher at Stns. E and F than at Stns. C and D in the middle part of the estuary. Salinity changes in the stations close to the river outfall (Stns. A and B) displayed also high temporal variations (Table 1). Therefore, sites with lower average salinity were subjected to greater fluctuation.

*Diversity of macrofauna*

A total of 70 species was collected at Akkeshi-ko estuary and Akkeshi Bay in three seasons of 2004 (Table 2). The mean annual species richness for total macrofauna was 14.6 $m^{-2}$ (± 1.8 SD). Annual average of species richness in *DF* group (9.2 $m^{-2}$ ± 1.2 SD) was higher than *SA* group (5.4 $m^{-2}$ ± 1.2 SD).

Occurrence patterns of each species were summarized by grouping six stations to three areas (mouth of river; Stns. A and B, center of estuary; Stns. C and D, and marine; Stns. E and F). A number as high as one third of species was captured in all the areas (35.7 %) whereas a quarter was recorded in the marine area (25.7 %). Species whose distribution was restricted to the river mouth (Stns. A and B: 2.9 %), and to Akkeshi-ko estuary (Stns. A, B, C and D: 7.1 %) were very few. This occurrence pattern was similar for both *SA* and *DF* groups.

Spatial and temporal variation in species richness, as well as interactions between time and station were significant except for the spatial variation in *DF* group (Table 3). In all seasons, the lowest species richness was observed in the unvegetated site (Stn. A) in the two faunal groups (Fig. 2). Between spring and summer, species richness in Akkeshi Bay (Stns. E and F) was higher than or similar to that in seagrass sites in the estuary (Stns. C and D) for both macrofaunal groups. In autumn, species richness was lower at Stn. F than Stns. C and D for *DF* group, whereas it was similar at all stations for *SA* group (Fig. 2).

### *Abundance of macrofauna*

A total of 222,015 individuals was collected at Akkeshi-ko estuary and Akkeshi Bay in three temporal terms of 2004. A gastropod, *Barleeia angustata*, was most abundant (Table 2). Two mysid species (*Neomysis awatschensis* and *N. mirabilis*) and two amphipod species (*Pontogeneia rostrata* and *Caprella mutica*) also occurred abundantly. These five species accounted for more than 90% of the total macrofaunal density.

The annual mean abundance in total macrofauna, *DF* and *SA* group was 4,111 inds. m$^{-2}$, 2,238 inds. m$^{-2}$ and 1,874 inds. m$^{-2}$, respectively. Variation in abundance among three replicates samples was generally lower in *DF* group than in *SA* group.

Spatial and temporal variation in abundance, and interaction between time and site were significant for the two groups (Table 3). In all sampling occasions, patterns in spatial abundance variation was much different between *DF* group and *SA* group (Fig. 3). For *DF* group, abundance tended to be higher at Stns. A and B than the other sites in spring, and it was higher at Stns. B-D than Stns. A, E and F in summer. In autumn, abundance at Stns. A and E was significantly lower than other stations. For *SA* group, patterns of spatial variation differed among seasons, although maximum abundance was observed at Stn. B in all seasons.

### *Similarity in macrofaunal composition*

Variations in similarity using the abundance and presence/absence data were significant both among sampling occasions and among sites for the two faunal (*DF* and *SA*) groups, whereas the global *R* among sites was higher than among sampling times (Table 4).

MDS plots showed different similarity patterns among the faunal groups and between the two data sets (abundance data and presence/absence data) (Fig. 4). MDS plots of the abundance data for *DF* group showed clear separation by sites. In contrast, a plot for *SA* group showed greater overlaps among sites. The presence/absence MDS plot was similar to that by abundance data for *DF* group although some sites were less clearly separated from each other (e.g., between Stns. C and E of total macrofauna, and between Stns. A and B of *DF* group) (Fig. 4). The *SA* group plot differed greatly from *DF* group because of a higher overlaps among sites. Regardless of data types and faunal groups, faunal similarity at unvegetated site (Stn. A) differed greatly from other seagrass meadow sites in all the analyses except for the presence/absence data for *DF* group where position of Stn. A overlaps greatly with that of Stn. B.

A significant negative relationship was detected between the similarity matrix (based on abundance data) and the salinity differences among pairs of six areas for *SA* group in summer, and for *DF* group in autumn (Table 5). For the similarity matrix based on the presence/absence data, significant negative correlation with salinity difference was found for both animal groups in autumn (Table 5).

## Discussion

Macrofaunal community structure in seagrass meadows of Akkeshi-ko estuary and Akkeshi Bay varied greatly among sites. Variation in salinity was related with some variables representing abundance and species richness of macrofauna, and their similarity among sites. However, the patterns of spatial variation in the macrofaunal community, as well as the degree of relatedness with salinity differed among sampling occasions, and among functional groups of organisms classified by its degree of association with seagrass substrates. These findings suggest that the salinity gradient plays an important role in the observed variation of the macrofaunal community structure in the seagrass meadows, but that its effects are complex, depending on other confounding factors and types of animals.

Species richness generally decreased with salinity in most faunal groups and in most occasions. Similar findings were reported in other estuarine systems where the number of macrofaunal species was correlated with salinity (Montagna & Kalke, 1992; Schlacher & Wooldridge, 1996; Mannino & Montagna, 1997; Edgar et al., 1999; Ysebaert et al., 2003). In earlier studies, variation in macrofaunal species composition in estuary system was discussed in relation to osmoregularity capacity, i.e., marine, brackish and freshwater species. It has been considered that high correlation between number of macrofaunal species and salinity is caused by the replacement of these groups (Remane, 1934; Remane & Schlieper, 1971). Whereas more recent studies argued that specific brackish water fauna do not exit, and that the salinity gradient in species richness is caused by the fact that fewer marine species can inhabit in lower salinities (Barnes, 1989; Hutchings, 1999). In the present study, few species were considered as freshwater or brackish species and increasing species richness of marine species toward the outer bay contributed to the observed relationships. In addition, MDS plots using the presence/absence data were less clearly separated by sites compared to those using abundance data, indicating that spatial variation of community structure of macrofauna may be caused by that of relative abundance among species rather than spatial replacement of the species.

In contrast to species richness, effects of the salinity gradient on abundance was not clear in most faunal groups. In addition, patterns of spatial variation changed with sampling occasions. Most notably in summer, abundance in seagrass meadows of Akkeshi-ko estuary (Stns. B-D) was much greater than the unvegetated area (Stn. A) and seagrass beds in marine area (Akkeshi Bay). This contradicts with the general tendency observed in the previous studies that found a trend from lower faunal abundance in upper estuaries areas to higher abundance in the more downstream areas (Schaffner et al., 1987; Montagna & Kalke, 1992; Dauer, 1993; Montague & Ley, 1993; Ysebaert et al., 1998; 2003). These studies have discussed that transported food and nutrients by river input stimulate primary production and consequently enhance abundance, biomass and production of faunal species in more euhaline areas of the estuaries (e.g., Nixon et al., 1986; Montagna & Yoon, 1991; Heip et al., 1995). In the case of our study area, primary productivity in summer is greater in seagrass beds than unvegetated areas in Akkeshi-ko estuary (Hasegawa et al., 2007; Hasegawa, N., unpublished). Productivity is also considered to be greater in Akkeshi-ko estuary than in Akkeshi Bay in summer due to higher summer water temperature and greater organic and inorganic input from rivers that are trapped in Akkeshi-ko estuaries (Oshima et al., 1999). Such factors can contribute to the enhanced abundance of macrofauna in summer in vegetated areas in Akkeshi-ko estuary. In fact, a population study on the mysid species (belonging to *DF* group) has revealed that dominant species like *Neomysis awatschensis* and *N. mirabilis* undergo repeated reproduction in Akkeshi-ko during summer months, and that *N. czerniawskii* migrates into Akkeshi-ko estuary from Akkeshi Bay in summer (Yamada et al., 2007). Such reproductive and migratory behaviors of the dominant species lead to the enhanced abundance of *DF* group. In spring and autumn, however, the effects of seagrass vegetation are not so pronounced due to the low temperature (*ca.* < 12 $^{o}$C) and small shoot size, and dominant macrofaunal species do not undergo reproduction during these seasons. Such combined effects of abiotic and biotic factors have resulted in complex time vs. site interactions in macrofaunal abundance.

One of the important findings in the present study is that patterns of spatial variation in diversity, abundance and similarity varied between the two functional groups that have different degrees of association with seagrass. Most notably, patterns of similarity varied greatly, as shown by more overlaps in sites in MDS plots for *SA* group compared to *DF* group. These results indicate that the effect of salinity gradient and other related factors operate differently on the two types of macrofauna. Species belonging to *DF* group can migrate more easily than *SA* group according to environmental factors such salinity gradient and other biological factors such as competition and predators. For example, three mysid species (*N. awatschensis*, *N. mirabilis* and *N. czerniawskii*) which are dominant species of *DF* group have different tolerances to salinity, and the population of each species change seasonally with different dispersal pattern between Akkeshi-ko estuary and Akkeshi Bay (Yamada et al., 2007). A grass shrimp, *P. latirostris* has low salinity tolerance, with a lower survivorship at salinities below 20 (Chiba et al., 2004), which may explain their absence in the upper part of Akkeshi-ko estuary (Stns. A and B). On the other hand, large overlaps in MDS plots for *SA* group indicate that species belonging to this group did not specialize to different requirements in estuarine environments. It is likely that only species with a tolerance to low salinity can inhabit Akkeshi-ko estuary although species-by-species examination for habitat requirement and life history traits are necessary to test this possibility.

Comparison between Stn. A (unvegetated site) and Stn. B (in seagrass meadow) provides information on the effects of seagrass vegetation on macrofaunal community because these two sites were subjected to similar environmental conditions at the river mouth. In most cases, abundance was lower at the unvegetated site, and MDS plots at the unvegetated site were far away from the other vegetated stations for both faunal groups except for the presence/absence data of *DF* group. This finding is consistent with those in previous studies showing higher diversity of macrofauna in seagrass meadows (Lewis, 1987; Edgar et al., 1994; Jernakoff et al., 1996; Hemminga & Duarte, 2000). We expected differences between the two sites were more pronounced for *SA* group that was more associated with seagrass than *DF* group. The difference in abundance was much greater for *SA* group as expected. However, species richness did not vary significantly for both groups between the two sites. This agrees with the general findings that most epifauna in seagrass beds exhibit little host specificity on seagrasses (Jernakoff et al., 1996; Hemminga & Duarte, 2000; Nakaoka, 2005). Some dominant species in *SA* group such as *Caprella mutica* and *Temanella turrita* were commonly found in other substrate types such as *Sargassum* beds and rocky bottoms in Akkeshi-ko estuary and Akkeshi Bay (Yamada, K. & M. Nakaoka, personal observation).

In conclusion, the present study demonstrated that macrofaunal community structures in seagrass beds varied with the salinity gradient of the Akkeshi-ko estuary and adjacent Akkeshi Bay, and that the pattern of spatial variation differed among seasons, and between functional groups of animals with different degree of dependence on seagrass substrates. However, it remains unknown if the observed variation along salinity gradient was due to direct effects of salinity, or other biotic/abiotic factors such as the variation in seagrass biomass, food availability and predation intensity that can also change with salinity. Concurrent monitoring of these unexamined factors as well as experimental analyses carefully manipulating these confounding factors are the next step toward the understanding the underlying mechanisms causing the variation in macrofaunal community in seagrass meadows along salinity gradient.

## Acknowledgements

We gratefully thank Captain S. Hamano, H. Katsuragawa and other staff of the Akkeshi Marine Station for assistance with the field collection. H. Mukai, C. Vallet, K. Takahashi, M. Kanamori, M. Watanabe, N. H. Kumagai and T. Takano helped with the species identification, analysis and discussion. M. Takahata and Y. Ishikawa of the Community Ecology Laboratory of Chiba University helped with the laboratory procedures and contributed to the fruitful discussions during the course of this study. A part of this research was financially supported by a Grant-in-Aid by Akkeshi Town for Scientific Research of Lake Akkeshi and Bekanbeushi Wetland to KY.

## References

Bonnet, E. & Y. Van de Peer, 2002. zt: a software tool for simple and partial Mantel tests. Journal of Statistical Software 7: 1-12.

Barnes, R. S. K., 1989. What, if anything, is a brackish-water fauna?. Transactions of the Royal Society of Edinburgh: Earth Sciences 80: 235-240.

Chiba, S., L. Aoki, & T. Ogata, 2004. Response of the pandalid shrimp *Pandalus latirostris* to dissolved oxygen, salinity and turbidity. Fisheries Science 70: 1174-1176.

Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Clarke, K. R. & R. N. Gorley, 2001. Primer v5: Primer-E Ltd.

Clarke, K. R. & R. M. Warwick, 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. 2nd edition: PRIMER-E, Plymouth, 172 pp.

Crawford, G. I., 1937. A review of the amphipod genus *Corophium*, with notes on the British species. Journal of the Marine Biological Association of the United Kingdom 21: 589-630.

Dauer, D. M., 1993. Biological criteria, environmental health and estuarine mcrobenthic community structure. Marine Pollution Bulletin 26: 249-257.

Day, J. H., 1981. Estuarine ecology, with particular reference to South Africa, A. A. Balkema, Rotterdam. 411 pp.

Day, R. W. & G. P. Quinn, 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59: 433-463.

Diaz, R. J. & R. J. Rosenberg, 1995. Marine benthic hypoxia; a review of its ecological effects and the behavioral responses of benthic macrofauna. Oceanography and Marine Biology: An Annual Review 33: 245-303.

Edgar, G. J. & M. Aoki, 1993. Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*. Oecologia 95: 122-133.

Edgar, G. J. & N. S. Barrett, 2002. Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables. Journal of Experimental Marine Biology and Ecology 270: 1-24.

Edgar, G. J., N. S. Barrett & P. R. Last, 1999. The distribution of macroinvertebrates and fishes in Tasmanian estuaries. Journal of Biogeography 26: 1169-1189.

Edgar, G. J., C. Shaw, G. F. Watson & L. S. Hammond, 1994. Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. Journal of Experimental Marine Biology and Ecology 176: 201-226.

Faith, D. P., P. R. Minchin & L. Belbin, 1978. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57-68.

Gambi, M. C., M. Lorenti, G. F. Russo, M. B. Scipione & V. Zupo, 1992. Depth and seasonal distribution of some groups of the vagile fauna of the *Posidonia oceanica* leaf stratum: structural and trophic analyses. PSZN Marine Ecology 13: 17-39.

Hamamoto, K. & H. Mukai, 1999. Effects of larval settlement and post-settlement mortality on the distribution pattern and abundance of the spirorbid tube worm *Neodexiospira brasiliensis* (Grube) (Polychaeta) living on seagrass leaves. PSZN Marine Ecology 20: 251-272.

Hasegawa, N., 2006. Studies on biological interactions and seagrass functions in a seagrass ecosystem. Ph.D. Thesis, Hokkaido Univ. Hokkaido, Japan.

Hasegawa N., H. Iizumi & H. Mukai, 2005. Nitrogen dynamics of the surfgrass *Phyllospadix iwatensis*. Marine Ecology Progress Series 293: 59-68.

Hasegawa, N., M. Hori & H. Mukai, 2007. Seasonal shifts in seagrass bed primary producers in a cold-temperate estuary: Dynamics of eelgrass *Zostera marina* and associated epiphytic algae. Aquatic botany 86: 337-345.

Hemminga, M. A. & C. M. Duarte, 2000. Seagrass Ecology. Cambridge University Press, Cambridge, 298 pp.

Heip, C. H. R., N. K. Goosen, P. M. J. Herman, J. Kromkamp, J. J. Middelburg & K. Soetaert, 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanography and Marine Biology: An Annual Review 33: 1-149.

Hutchings, P., 1999. Taxonomy of estuarine invertebrates in Australia. Australian Journal of Ecology 24: 381-394.

Iizumi, H., S. Taguchi, T. Minami, H. Mukai & S. Maekawa, 1995. Distribution and variability nutrients, chlorophyll *a*, particulate organic matters, and their carbon and nitrogen contents, in Akkeshi-ko, an estuary in northern Japan. Bulletin of the Hokkaido National Fisheries Research Institute 59: 43-67.

Jernakoff, P., A. Brearley & J. Nielsen, 1996. Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanography and Marine Biology: An Annual Review 34: 109-162.

Kanamori, M., S. Goshima & H. Mukai, 2004. Seasonal variation in host utilization of epiphytic *Lacuna* species in mixed algal and surfgrass stands in Japan. PSZN Marine Ecology 25: 51-69.

Kasim, M. & H. Mukai, 2006. Contribution of benthic and epiphytic diatoms to clam and oyster production in the Akkeshi-ko estuary. Journal of Oceanography 62: 267-281.

Kikuchi, T., 1966. An ecological study on animal communities of the *Zostera marina* belt in Tomioka Bay, Amakusa, Kyushu. Publications of Amakusa Marine Biological Laboratory 1: 1-106.

Komai, T., 1999. A revision of the genus *Pandalus* (Crustacea: Decapoda: Caridea: Pandalidae). Journal of Natural History 33: 1265-1372.

Lewis, F. G., 1987. The crustacean epifauna of seagrass and macroalgae in Apalachee Bay, Florida, USA. Marine Biology 94: 219-229.

Mannino, A. & P. A. Montagna, 1997. Small-scale spatial variation of macrobenthic community structure. Estuaries 20: 159-173.

Mauchline, J., 1980. The biology of mysids and euphausiids. Advances in Marine Biology 18: 1-681.

McNeill, S. E. & J. D. Bell, 1992. Comparison of beam trawls for sampling macrofauna of *Posidonia* seagrass. Estuaries 15: 360-367.

Miyake, S., 1982. Japnease crustacean decapods and stomatopods in color. I - Macrura, Anomura and Stomatopoda. Hoikusha Publishing Co, LTD, Osaka, Japan: 261 pp.

Montague, C. L. & J. A. Ley, 1993. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in Northeastern Florida Bay. Estuaries 16: 703-717.

Montagna, P. A. & R. D. Kalke, 1992. The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. Estuaries 15: 307-326.

Montagna, P. A. & W. B. Yoon, 1991. The effect of freshwater inflow on meiofaunal consumption of sediment bacteria and microphytobenthos in San Antonio Bay, Texas, USA. Estuarine, Coastal and Shelf Science 33: 529-547.

Mukai, H., 1971. The phytal animals on the thalli of *Sargassum serratifolium* in the *Sargassum* region, with reference to their seasonal fluctuations. Marine Biology 8: 170-182.

Mukai, H., 1990. Interspecific competition on refuges among the grass shrimps living on *Zostera* leaves and a role of carnivore on the competition. Benthos Research 39: 9-14. (in Japanese with English abstract)

Murano, M., 1963. Fisheries biology of a marine relict mysid *Neomysis intermedia* Czerniawsky II. On the food habits. Suisanzoshoku 11: 159-165. (in Japanese)

Nakaoka, M., 2003. Predation on seeds of seagrasses *Zostera marina* and *Zostera caulescens* by a tanaid crustacean *Zeuxo* sp. Aquatic Botany 72: 99-106.

Nakaoka, M., 2005. Plant-animal interactions in seagrass beds: ongoing and future challenges for understanding population and community dynamics. Population Ecology 47: 167-177.

Nakaoka, M., T. Toyohara & M. Matsumasa, 2001. Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuchi Bay, Japan. PSZN Marine Ecology 22: 379-395.

Nixon, S. W., C. A. Oviatt, J. Frithsen & B. Sullivan, 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. Journal of the Limnological Society of South Africa 12: 43-71.

Oshima, Y., M. J. Kishi & T. Sugimoto, 1999. Evaluation of the nutrient budget in a seagrass bed. Ecological Modelling 115: 19-33.

Ohtsuka, S., H. Inagaki, T. Onbe, K. Gushima & Y. H. Yoon, 1995. Direct observations of groups of mysids in shallow coastal waters of western Japan and southern Korea. Marine Ecology Progress Series 123: 33-44.

Oishi, K. & M. Saigusa, 1999. Rhythmic patterns of abundance in small sublittoral crustaceans: variety in the synchrony with day/night and tidal cycles. Marine Biology 133: 237-247.

Orth, R. J., K. L. Heck Jr. & J. V. Montfrans, 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7: 339-350.

Pelegri, S. P., L. P. Nielsen & T. H. Blackburn, 1994. Denitrification in estuarine sediment stimulated by the irrigation activity of the amphipod *Corophium volutator*. Marine Ecology Progress Series 105: 285-290.

Quinn, G. P. & M. J. Keough, 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, 537 pp.

Remane, A., 1934. Die Brackwasserfauna. Zoologischer Anzeiger (Supplement) 7: 34-74.

Remane, A. & C. Schlieper, 1971. Biology of brackish waters. Wiley Inter-Sicience, New York. 373 pp.

Saigusa, M., K. Oishi, A. Ikumoto, H. Iwasaki & M. Terajima, 2000. Emergence patterns of small subtidal arthropods in relation to day/night, tidal, and surface/bottom factors: investigations in the boreal sea, Japan (Akkeshi, Hokkaido). Journal of Oceanography 56: 295-310.

Sasil-Orbita, M. L. & H. Mukai, 2006. A comparative study of the photosynthetic activity among three temperate seagrass species in Northern Japan. Marine Ecology 27: 388-396.

Sawamura, M., 2000. Fish-benthos foodweb structure at the *Phyllospadix iwatensis* seagrass bed, Hokkaido, Japan. Aquabiology 131: 542-549. (in Japanese with English abstract)

Schaffner, L. C., R. J. Diaz, C. R. Olsen & I. L. Larsen, 1987. Faunal characteristics and sediment accumulation processes in the James River estuary, Virginia. Estuarine, Coastal and Shelf Science 25: 211-226.

Schlacher, T. A. & T. H. Wooldridge, 1996. Axial zonation patterns of subtidal macrozoobenthos in the Gamtoos estuary, South Africa. Estuaries 19: 680-696.

Smith, F. & J. D. Witman, 1999. Species diversity in subtidal landscapes: Maintenance by physical processes and larval recruitment. Ecology 80: 51-69.

Tayasu, I., N. Shigesada, H. Mukai & H. Caswell, 1999. Predator-mediated coexistence of epiphytic grass shrimps that compete for refuges. Ecological Modeling 84: 1-10.

Toyohara, T., M. Nakaoka & K. Aioi, 1999. Population dynamics and reproductive traits of phytal gastropods in seagrass bed in Otsuchi Bay, North-Eastern Japan. PSZN Marine Ecology 20: 273-289.

van Katwijk, M. M., G. H. W. Schmitz, A. P. Gasseling & P. H. van Avesaath, 1999. Effects of salinity and nutrient load and their interaction on *Zostera marina*. Marine Ecology Progress Series 190: 155-165.

Watanabe, M., M. Nakaoka & H. Mukai, 2005. Seasonal variation in vegetative growth and production of the endemic Japanese seagrass *Zostera asiatica*: a comparison with sympatric *Zostera marina.* Botanica Marina 48: 266-273.

Williams, W. D., A. J. Boulton & R. G. Taaffe, 1990. Salinity as a determinant of salt lake fauna: a question of scale. Hydrobiologia 197: 257-266.

Yamada, K., K. Takahashi, C. Vallet, S. Taguchi & T. Toda, 2007. Distribution, life history and production of three species of *Neomysis* in Akkeshi-ko estuary, northern Japan. Marine Biology 150: 905-917.

Yamashita, K. & K. Hayashi, 1984. Larvae of Decapoda Macrura in the vicinity of Miyazima Aquarium, Miyazima, the Seto Inland Sea, III. *Eualus leptognathus* (Stimpson) (Caridea, Hippolytidae). Proceedings of the Japanese Society of Systematic Zoology 28: 19-28. (in Japanese with English abstract)

Ysebaert, T., P. Meire, J. Coosen & K. Essink, 1998. Zonation of intertidal macrobenthos in the estuaries of Schelde and Ems. Aquatic Ecology 32: 53-71.

Ysebaert, T., P. M. J. Herman, P. Meire, J. Craeymeersch, H. Verbeek & C. H. R. Heip, 2003. Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. Estuarine, Coastal and Shelf Science 57: 335-355.

Yu, O. H., H. Y. Soh & H. L. Suh, 1999. Seasonal zonation patterns of benthic amphipods in a sandy shore surf zone of Korea. Journal of Crustacean Biology 22: 459-466.

Zelickman, E. A., 1974. Group orientation in *Neomysis mirabilis* (Mysidacea: Crustacea). Marine Biology 24: 251-258.

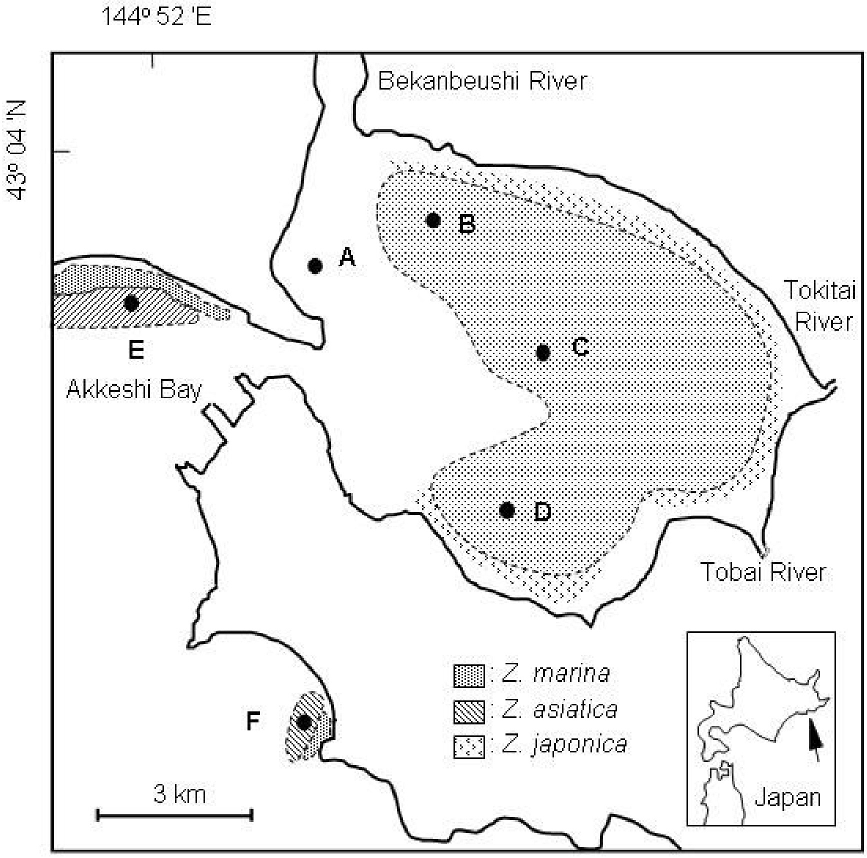

Fig. 1

Fig. 1. Study sites at Akkeshi-ko estuary (Stns. A-D) and Akkeshi Bay (Stns. E and F). Shaded areas indicate vegetation cover of the three *Zostera* species.

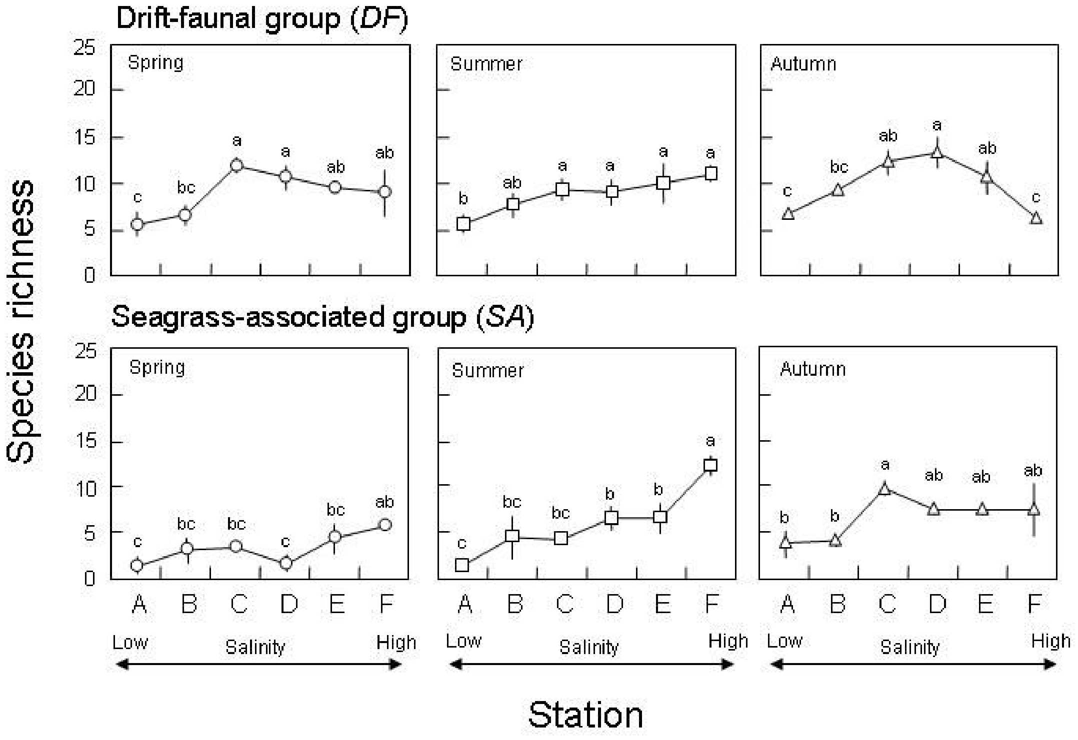

Fig. 2

Fig. 2. Spatial and temporal variation in species richness of two functional groups (drift-faunal group and seagrass-associated group) in Akkeshi-ko estuary and Akkeshi Bay. Bars indicate SD of the three replicated samples. Different letters denote a pair of sites with significant differences detected using Tukey post-hoc comparisons.

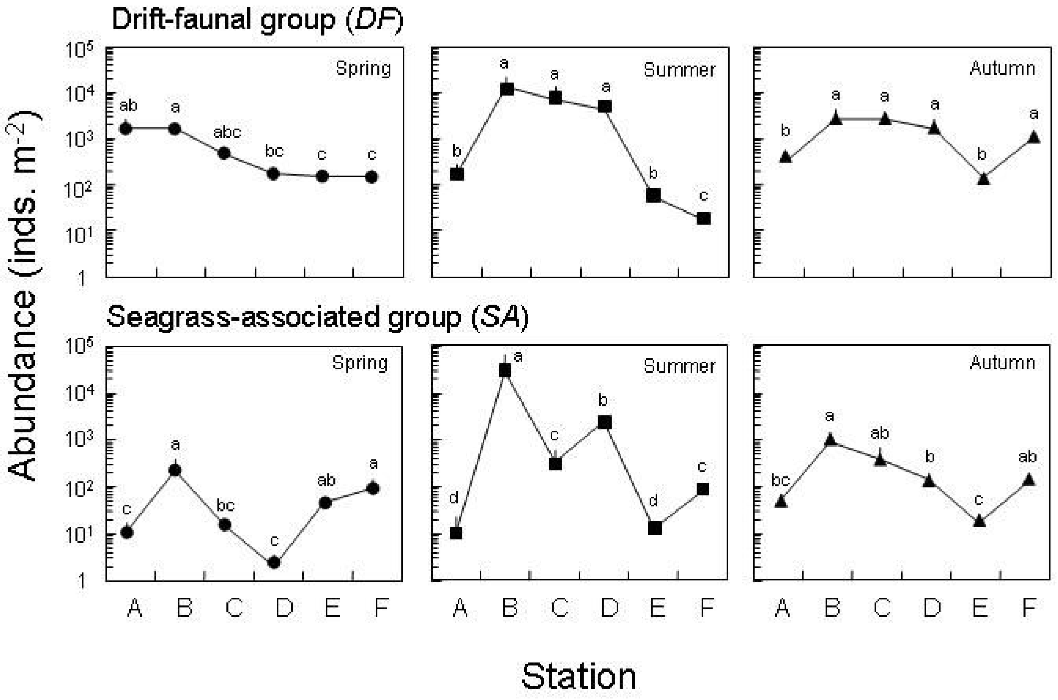

Fig. 3

Fig. 3. Spatial and temporal variation in abundance of two functional groups (drift-faunal group and seagrass-associated group) in Akkeshi-ko estuary and Akkeshi Bay. Bars indicate 0.5 SD of the three replicated samples. Different letters denote a pair of sites with significant differences detected by Tukey post-hoc comparisons.

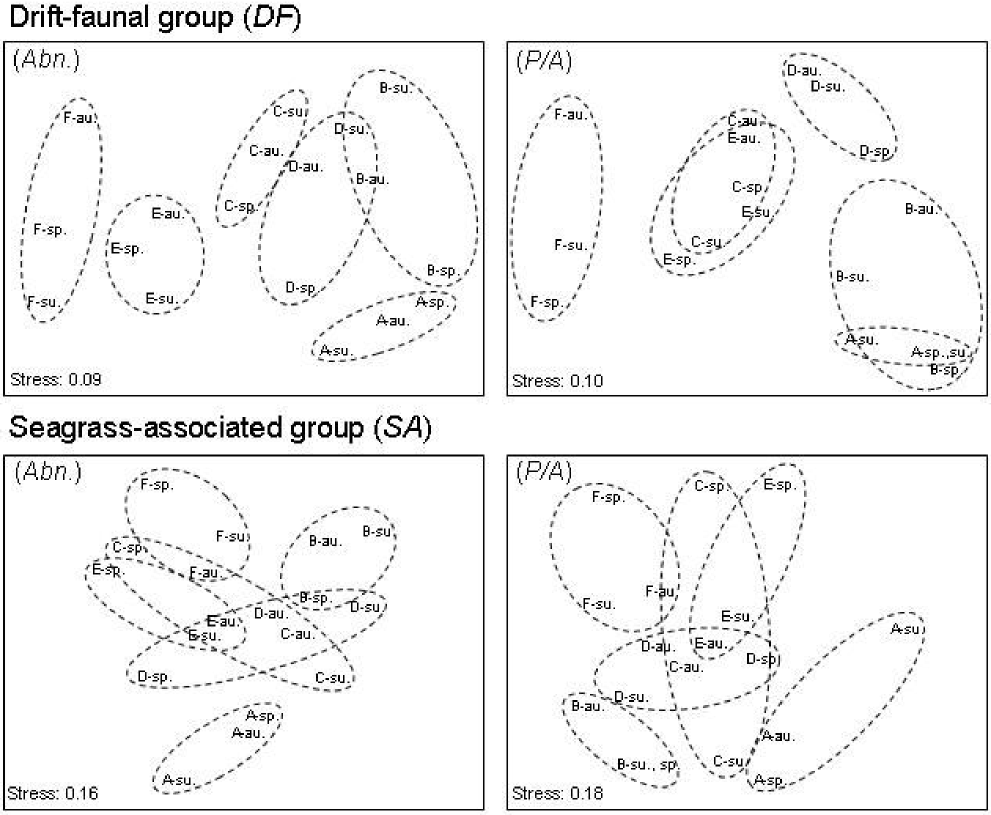

Fig. 4

Fig. 4. Results of MDS plots showing similarity of community structure in different sites (Stns. A-F) and seasons (sp.; spring, su.; summer and au.; autumn) for each faunal group (drift-faunal group and seagrass-associated group). Bray-Curtis similarities were calculated based on double-square root of abundance (*Abn.*) and the presence/absence of each taxon (*P/A*) for the analysis.

Table 1. Mean, median values and standard deviation of salinity recorded from 1993 to 2005 at each station of Akkeshi-ko estuary and Akkeshi Bay in each season. Averaged salinity **(Bold type)** for each season and site was used for analysis of this study due to reducing possible biases of data taken at abnormal conditions.

| Season | Year | Stations | | | | | | References |
|---|---|---|---|---|---|---|---|---|
| | | A | B | C | D | E | F | |
| Spring | 1993 | 7.7 | 25.2 | 24.5 | 20.4 | 26.7 | - | Iizumi et al. (1995)[a] |
| | 1997 | 18.6 | 27.9 | 27.0 | 26.3 | 29.5 | 31.8 | Yamada et al. (2007)[b] |
| | 2001 | - | - | - | - | - | 24.0 | Watanabe et al. (2005)[b] |
| | 2004 | 22.7 | 25.0 | 26.8 | 24.5 | 27.4 | 28.9 | This study[b] |
| | 2005 | - | 27.1 | 29.0 | 27.0 | 29.4 | - | Tanaka et al. (unpubl.)[c] |
| | **Average** | **16.3** | **26.3** | **26.8** | **24.5** | **28.3** | **28.2** | |
| | Median | 17.5 | 26.3 | 26.8 | 24.5 | 28.3 | 28.6 | |
| | SD | 7.8 | 1.4 | 1.8 | 3.0 | 1.4 | 3.9 | |
| Summer | 1993 | 2.0 | 11.8 | 22.8 | 23.1 | 25.2 | - | Iizumi et al. (1995)[a] |
| | 1997 | 10.3 | 12.7 | 29.1 | 26.0 | 26.9 | 30.9 | Yamada et al. (2007)[b] |
| | 2001 | - | - | - | - | - | 30.7 | Watanabe et al. (2005)[b] |
| | 2005 | - | 20.9 | 29.1 | 26.0 | 31.0 | - | Tanaka et al. (unpubl.)[c] |
| | **Average** | **6.2** | **15.1** | **27.0** | **25.0** | **27.7** | **30.8** | |
| | Median | 6.2 | 13.9 | 28.0 | 25.5 | 27.3 | 30.8 | |
| | SD | 5.9 | 5.0 | 3.7 | 1.7 | 3.0 | 0.1 | |
| Autumn | 1993 | 26.3 | 23.5 | 26.8 | 25.1 | 29.3 | - | Iizumi et al. (1995)[a] |
| | 1997 | 8.3 | 20.8 | 29.0 | 27.9 | 29.2 | 32.9 | Yamada et al. (2007)[b] |
| | 2001 | - | - | - | - | - | 33.0 | Watanabe et al. (2005)[b] |
| | 2005 | 16.6 | - | 28.2 | 29.9 | 32.2 | 32.9 | Tanaka et al. (unpubl.)[c] |
| | **Average** | **13.6** | **19.8** | **27.6** | **26.0** | **28.7** | **32.2** | |
| | Median | 15.1 | 20.8 | 27.9 | 26.9 | 29.2 | 32.9 | |
| | SD | 9.0 | 1.9 | 1.2 | 2.4 | 1.8 | <0.1 | |

tom and surface during the daytime by T-S meter.

[b] At every 0.5 m above the bottom during the daytime by T-S meter.

[c] At 0.3 m above the bottom in during several days by Alec. COMPACT-CT (every 1-10 min.)

Table 2. Occurrence pattern of a total of 70 species among regions in Akkeshi-ko estuary and Akkeshi Bay.

| Species | Rank | Average abundance (inds. m$^{-2}$) | Proportion (%) | Faunal type | Spatial occurrence | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | A | B | C | D | E | F |
| **Amphipoda** | | | | | | | | | | |
| *Pontogeneia rostrata* | 4 | 369.07 | 8.99 | *DF* | + | + | + | + | + | + |
| *Caprella mutica* | 5 | 121.60 | 2.96 | *SA* | + | | + | + | + | + |
| *Ampithoe lacertosa* | 8 | 34.53 | 0.84 | *SA* | + | + | + | | + | + |
| *Grandidierella japonica* | 9 | 30.93 | 0.75 | *DF* | + | + | + | + | + | + |
| *Corophium acherusicum* | 10 | 26.49 | 0.65 | *DF* | + | + | + | + | + | |
| *Ischyrocerus anguipes* | 13 | 14.89 | 0.36 | *SA* | | | + | | + | + |
| *Caprella penantis* (S type) | 14 | 14.61 | 0.36 | *SA* | + | + | | + | | + |
| *Pleustes panopla* | 17 | 12.36 | 0.30 | *SA* | | + | + | + | | + |
| *Photis reinhardi* | 18 | 8.41 | 0.20 | *DF* | | + | | + | | |
| *Caprella gigantochir* | 19 | 7.78 | 0.19 | *SA* | | + | + | | | |
| *Aoroides columbiae* | 20 | 7.04 | 0.17 | *SA* | | + | + | + | | + |
| *Ampithoe* sp. | 21 | 5.49 | 0.13 | *SA* | + | + | + | + | + | + |
| *Eogammarus* sp. | 22 | 4.61 | 0.11 | *DF* | + | + | | | | |
| *Corphium* sp. | 24 | 3.51 | 0.09 | *DF* | + | + | | + | + | |
| *Hyale* sp. | 27 | 2.10 | 0.05 | *SA* | | + | + | | + | + |
| *Caprella kroyeri* | 28 | 1.98 | 0.05 | *SA* | | | | + | | |
| *Grandidierella* sp. | 29 | 1.48 | 0.04 | *DF* | | | + | | | + |
| *Metaphoxus* sp. | 31 | 1.42 | 0.03 | *DF* | | | | + | | |
| *Synchelidium lenorstalum* | 33 | 1.08 | 0.03 | *DF* | | | + | + | + | |
| *Aoroides* sp. 1 | 34 | 1.04 | 0.03 | *SA* | + | | + | | + | |
| *Aoroides longimerus* | 35 | 0.93 | 0.02 | *SA* | | | + | | | |
| *Metopa* sp. | 37 | 0.71 | 0.02 | *SA* | | | + | + | + | + |
| *Caprella scaura* | 38 | 0.71 | 0.02 | *SA* | | | + | | | + |
| *Orchomene* sp. | 40 | 0.52 | 0.01 | *DF* | | + | | + | | |
| *Caprella laeviuscula* | 41 | 0.44 | 0.01 | *SA* | | | | | | + |
| *Caprella polyacantha* | 42 | 0.36 | 0.01 | *SA* | | | + | | + | + |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Caprella tsugarensis* | 43 | 0.36 | 0.01 | *SA* | + | | | + | | |
| *Pleusirus secorrus* | 44 | 0.26 | 0.01 | *DF* | | | | + | | |
| *Hyale barbicornis* | 47 | 0.12 | <0.01 | *SA* | | + | | | | |
| *Allorchestes* sp. | 48 | 0.09 | <0.01 | *SA* | | | | + | | + |
| *Urothoe grimaldii japonica* | 50 | 0.06 | <0.01 | *DF* | | | | + | | |
| *Caprella danilevskii* | 52 | 0.04 | <0.01 | *SA* | | | | | | + |
| *Caprella bispinosa* | 53 | 0.03 | <0.01 | *SA* | | | | | | + |
| *Stenothoe* sp. | 54 | 0.03 | <0.01 | *SA* | | | | | | + |
| *Aoroides* sp. 2 | 55 | 0.02 | <0.01 | *SA* | | | | | | + |
| *Monoculodes* sp. | 59 | 0.01 | <0.01 | *DF* | | | | | | + |
| *Byblis japonicus* | 61 | 0.01 | <0.01 | *DF* | | | | | + | |
| | | | | | | | | | | |
| **Decapoda** | | | | | | | | | | |
| *Crangon* sp. | 11 | 20.36 | 0.50 | *DF* | + | + | + | + | + | + |
| *Spirontocaris ochotensis* | 23 | 3.76 | 0.09 | *DF* | | | + | + | + | + |
| *Pandalopsis pacifica* | 25 | 3.32 | 0.08 | *DF* | | + | | + | + | + |
| *Heptacarpus grebnitzkii* | 30 | 1.46 | 0.04 | *DF* | | + | + | + | + | + |
| *Heptacarpus rectirostris* | 45 | 0.20 | <0.01 | *DF* | | + | + | + | + | + |
| *Pandalus kessleri* | 46 | 0.18 | <0.01 | *DF* | | | + | | + | + |
| *Eualus leptognathus* | 51 | 0.05 | <0.01 | *DF* | | | + | | + | + |
| *Heptacarpus* sp. | 58 | 0.02 | <0.01 | *DF* | | | | | + | + |
| *Lebbeus speciosus* | 63 | 0.01 | <0.01 | *DF* | | | + | | | |
| *Sergia lucens* | 66 | <0.01 | <0.01 | *DF* | | | | | | + |
| | | | | | | | | | | |
| **Gastropoda** | | | | | | | | | | |
| *Barleeia angustata* | 1 | 1590.45 | 38.75 | *SA* | | + | + | + | + | + |
| *Temanella turrita* | 7 | 34.82 | 0.85 | *SA* | + | + | + | + | + | + |
| *Reticunassa acutidentatus* | 26 | 2.20 | 0.05 | *DF* | | | + | + | + | |
| *Lacuna decorata* | 49 | 0.09 | <0.01 | *SA* | | + | + | + | + | + |
| *Reticunassa fratercula hypolia* | 56 | 0.02 | <0.01 | *DF* | | | | | | + |
| *Retusa* sp. | 57 | 0.02 | <0.01 | *DF* | | | | | | + |
| *Lirularia iridescens* | 60 | 0.02 | <0.01 | *SA* | | | + | | + | + |
| *Batillaria multiformis* | 67 | <0.01 | <0.01 | *DF* | | + | + | | | |
| *Lacuna uchidai* | 69 | <0.01 | <0.01 | *SA* | | | | | | + |
| *Margarites pilsbryi* | 70 | <0.01 | <0.01 | *SA* | | | | | | + |

|  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
| **Mysida** |  |  |  |  |  |  |  |  |  |  |
| *Neomysis awatschensis* | 2 | 977.70 | 23.80 | *DF* | + | + | + | + | + |  |
| *Neomysis mirabilis* | 3 | 709.05 | 17.27 | *DF* | + | + | + | + | + |  |
| *Acanthomysis schrencki* | 6 | 36.62 | 0.89 | *DF* | + |  | + | + | + | + |
| *Neomysis czerniawskii* | 15 | 14.36 | 0.35 | *DF* |  | + | + | + | + |  |
| *Exacanthomysis japonica* | 16 | 13.26 | 0.32 | *DF* |  |  | + | + |  |  |
| *Nipponomysis toriumii* | 39 | 0.54 | 0.01 | *DF* |  |  |  |  |  | + |
| *Acanthomysis* sp. | 64 | 0.01 | 0.01 | *DF* |  |  |  |  | + | + |
|  |  |  |  |  |  |  |  |  |  |  |
| **Isopoda and Tanaida** |  |  |  |  |  |  |  |  |  |  |
| *Cymodoce japonica* | 12 | 18.74 | 0.46 | *SA* | + | + | + | + | + | + |
| *Idotea ochotensis* | 32 | 1.36 | 0.03 | *SA* | + | + | + | + | + | + |
| *Paranthura japonica* | 36 | 0.82 | 0.02 | *SA* |  |  | + | + |  |  |
| *Idotea* sp. | 62 | 0.01 | <0.01 | *SA* |  |  |  |  |  | + |
| *Zeuxo* sp. | 65 | <0.01 | <0.01 | *SA* |  |  |  |  |  | + |
| *Tecticeps glaber* | 68 | <0.01 | <0.01 | *SA* |  |  |  |  | + |  |

Table 3. Results of two-way ANOVA testing spatial and seasonal variation in species richness (number of species $m^{-2}$) and abundance (log transformed inds. $m^{-2}$) of two macrofaunal groups (*DF* and *SA*).

| Factor | df | MS | *F* | *P* | Factor | df | MS | *F* | *P* |
|---|---|---|---|---|---|---|---|---|---|
| Species richness (number of species $m^{-2}$) |  |  |  |  | Abundance (log transformed inds. $m^{-2}$) |  |  |  |  |
| Drift faunal group |  |  |  |  | Drift faunal group |  |  |  |  |
| Season | 2 | 5.17 | 1.97 | <0.001 | Season | 2 | 0.62 | 8.7 | <0.001 |
| Site | 5 | 36.52 | 13.89 | 0.155 | Site | 5 | 3.47 | 48.75 | 0.001 |
| Season × Site | 10 | 8.19 | 3.11 | 0.006 | Season × Site | 10 | 1.08 | 15.17 | <0.001 |
| Error | 36 | 2.63 |  |  | Error | 36 | 0.07 |  |  |

|  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
| Seagrass associated group (*SA*) |  |  |  |  | Seagrass associated group (*SA*) |  |  |  |  |
| Season | 2 | 66.5 | 23.94 | <0.001 | Season | 2 | 4.47 | 29.54 | <0.001 |
| Site | 5 | 40.03 | 14.41 | <0.001 | Site | 5 | 3.91 | 25.83 | <0.001 |
| Season × Site | 10 | 11.17 | 4.02 | 0.001 | Season × Site | 10 | 1.52 | 10.02 | <0.001 |
| Error | 36 | 2.78 |  |  | Error | 36 | 0.15 |  |  |

Table 4. Results of ANOSIM testing among-season and among-site variations in similarity of two functional group (*DF* and *SA*). The test was carried for similarity data obtained for the two types of data (abundance and presence/absence).

| Faunal group | Among seasons |  | Among sites |  |
|---|---|---|---|---|
|  | Global *R* | *P* | Global *R* | *P* |
| Abundance (transformed) |  |  |  |  |
| Drift faunal group (*DF*) | 0.850 | < 0.001 | 0.956 | < 0.001 |
| Seagrass associated group (*SA*) | 0.508 | < 0.001 | 0.654 | < 0.001 |
| Presence / Absence |  |  |  |  |
| Drift faunal group (*DF*) | 0.567 | < 0.001 | 0.886 | < 0.001 |
| Seagrass associated group (*SA*) | 0.375 | < 0.001 | 0.526 | < 0.001 |

Table 5. Results of Mantel test (*r*) betweensimilarity matrices of two macrofaunal groups (*DF* and *SA*) and differential salinity matrix for pairs of stations.

| Faunal group | Spring | | Summer | | Autumn | |
|---|---|---|---|---|---|---|
| | *r* | *P* | *r* | *P* | *r* | *P* |
| Abundance (transformed) | | | | | | |
| Drift faunal group (*DF*) | -0.235 | 0.086 | -0.155 | 0.267 | -0.782 | 0.006 |
| Seagrass associated group (*SA*) | -0.318 | 0.031 | -0.572 | 0.021 | -0.441 | 0.069 |
| Presence / Absence | | | | | | |
| Drift faunal group (*DF*) | -0.014 | 0.306 | -0.431 | 0.096 | -0.902 | 0.003 |
| Seagrass associated group (*SA*) | -0.312 | 0.050 | -0.522 | 0.143 | -0.567 | 0.028 |