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Effects of hypoxia on principal prey and growth of flathead flounder *Hippoglossoides dubius* in Funka Bay, Japan

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ABSTRACT: Effects of hypoxia on the principal prey and growth of flathead flounder *Hippoglossoides dubius* were studied in Funka Bay. Of the three dominant year-classes that occurred in recent years, the 1995 year-class was small in total length at age ≥ 3 and low in condition factor at age ≥ 2. Ophiuroids (almost *Ophiura sarsi*), which were the dominant prey in the 1980s, were of little importance and instead, crustaceans such as mysids, natant decapods and pelagic amphipods, bivalves and fish were important prey items for *H. dubius* in 2000–2001. In addition, the feeding intensity of *H. dubius* in 2000–2001 was lower than that in the 1980s. These facts are closely related to a reduction of prey abundance, particularly ophiuroids. It seems that the hypoxia that occurred in the central part of the bay during the summer and autumn of 1995–1997 caused the poor food supply and low growth rate at ages 2–4 of the 1995 year-class.

KEY WORDS: **condition factor, feeding, flathead flounder, Funka Bay, growth, *Hippoglossoides dubius*, hypoxia, ophiuroids.**

INTRODUCTION

Hypoxic events affect the existence of many sea animals seriously.[1–3] Many studies have been conducted on the survival times of marine benthos under hypoxic conditions (e.g. Vetter *et al.*[4]). In recent years, the effects of hypoxia on growth, feeding and metabolism have been reported by several authors, for example in fish, Atlantic cod *Gadus morhua*,[5] mudskippers *Boleophthalmus boddaerti and Periophthalmodon schlosser*[6,7] and sole *Solea solea*,[8,9] and also in ophiuroid *Amphiura filiformis*,[10,11] bivalves *Crassostrea virginica*[12] and *Mytilus edulis*,[13] white shrimp *Penaeus setiferus*[14] and polychaete *Capitella* sp.[15] These studies are based upon only the results of the laboratory experiments.

Some field studies (e.g. Imabayashi,[16] Kikuchi,[17] Pearson *et al.*[18] Josefson and Widbom,[19] Furota[20]) demonstrated the reductions of biomass and abundance in benthos assemblages in the areas with low oxygen concentrations. As for fish, Pihl,[21] Pihl *et al.*[22,23] and Baden *et al.*[24] reported that some demersal fish species left the areas with low oxygen concentrations and changed diet. However, there are few studies on a change in growth caused by reduced oxygen concentration.[3]

In Funka Bay, Hokkaido, bottom water with an oxygen concentration of ≤1.5 mL/L had not been observed until the 1980s.[25,26] However, severe hypoxia (0.6–1.1 mL/L) occurred in the central part of the bay during the summer and autumn of 1995–1997,[27] and the abundances of flathead flounder *Hippoglossoides dubius* and coonstripe shrimp *Pandalus hypsinotus* decreased drastically in the hypoxic area.[28]

Hippoglossoides dubius is the main component in the demersal fish community and is an important fishery resource in Funka Bay. For this reason, many investigations have been conducted on distribution and annual life cycle,[29–31] food habits,[32,33] age and growth,[34] food organisms[33,35] and annual change in year-class strength.[36] However, no information is available on the effects of hypoxia on the biological production of *H. dubius*. The purpose of the present paper is to estimate the effects of a hypoxic event on the principal prey and growth of *H. dubius* in Funka Bay.

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MATERIALS AND METHODS

Study area

Funka Bay is located at the south-western part of Hokkaido, and is a semi-enclosed inner bay with a basin with a maximum depth of 96 m (Fig. 1). The characteristics of hydrographic conditions are as follows: in spring, the Oyashio Coastal Water (1–3°C, 33.0–33.3‰) flows into the bay and stagnates during summer. The intrusion of the Tsugaru Warm Water (≥6°C, ≥33.8‰) occurs in autumn and stagnates during winter. The annual bottom water temperatures in the basin range from 2°C to 10°C.[36–39] The silt (Md$\Phi \geq 6$) accumulates in the greater part of the bay and the distribution of sand–gravel is limited to off Muroran.[40] In recent years, the progress of eutrophication in the central part of the bay has been suggested.[41]

Sampling and data analysis

Samplings were conducted using R/V *Ushio-Maru* of Faculty of Fisheries, Hokkaido University in the daytime (09:00–16:30) from August 1993 to November 2001 in Funka Bay (Table 1; Fig. 1). *Hippoglossoides dubius* were collected with a 24-m otter trawl net (cod end liner of 12 mm mesh). The trawl net was towed at speeds of approximately 3 knots for 15 min on the sea bottom at each sampling station. Collections of benthic invertebrates were conducted with a sledge net using a 1-m × 1.5-m frame (cod end mesh of 3 mm) in June and October–November 2000 and May 2001. The sledge net was towed at speeds of approximately 2 knots for 1.5–5 min on the sea bottom. The samples were washed onto a 3-mm aperture sieve screen on the ship, and retained fractions were fixed in 10% buffered formalin seawater. After August 2000 the water samples at approximately 0.3 m above the

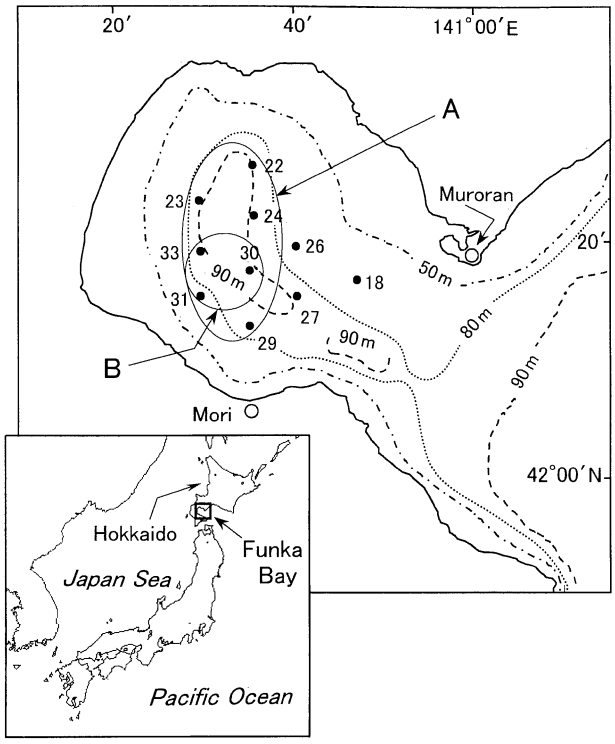

Fig. 1 Sampling sites and contours of depth in Funka Bay. (●) Sledge net towing station; A, area for investigating growth and condition factor; B, area for investigating food habits. Numerals denote station number.

Table 1 Samples of *Hippoglossoides dubius* and benthic invertebrates

	H. dubius†		Benthic invertebrates‡
Sampling date	Station no.	No. fish	Station no.
31 Aug.–2 Sep. 1993	22, 30	263	
3–5 Oct. 1994	29, 30	277	
29–30 Aug. 1995	29, 30	245	
26–28 Aug. 1996	23, 24, 29, 30, 31	606	
27–28 Aug. 1997	23, 24, 29, 30, 31	1051	
26–27 Aug. 1998	24, 29, 30, 31	525	
1 Sep. 1999	29, 30	267	
29–30 June 2000	–	0	18, 24, 26, 27, 29, 30, 31, 33
22–24 Aug. 2000	24, 29, 30, 31, 33	783	
17 Oct.–2 Nov. 2000	24, 30, 31, 33	233	18, 24, 26, 27, 29, 30, 31, 33
12–14 Mar. 2001	30, 33	257	
28–30 May 2001	30, 33	260	18, 23, 24, 26, 27, 29, 30, 31, 33
31 Oct.–2 Nov. 2001	24, 30, 31, 33	930	

†Sampled with an otter trawl net.
‡Sampled with a sledge net.

sea bottom were collected using a Van-Dorn bottle (6.8 L), and the dissolved oxygen concentration was measured by the Winkler method.

In the laboratory, *H. dubius* were sexed and recorded along with total length (mm), wet body weight and gonad weight (nearest 0.1 g) after thawing. The age was determined from the annuli of otolith, according to Nakatani *et al.*[34] Stomachs of *H. dubius* collected from August 2000 to May 2001 were excised and preserved in 10% buffered formalin solution. All food organisms in the stomachs and sledge net samples were identified to the lowest taxon possible, counted and wet weighed (nearest 0.01 g). For comparison of data by fish sizes, we divided the sampled *H. dubius* into four length groups: ≤200 mm, 201–250 mm, 251–300 mm and ≥301 mm total length. Diets were analyzed in terms of numerical composition (%*N*), weight composition (%*W*) and frequency of occurrence (%*F*):

$$\%N_i = n_i \times 10^2 / \sum_{i=1}^{n} n_i$$

$$\%W_i = w_i \times 10^2 / \sum_{i=1}^{n} w_i$$

$$\%F_i = f_i \times 10^2 / \sum_{i=1}^{n} f_i$$

where n is the total number of prey items found in a unit, n_i and w_i are the number and total wet weight of prey items i in a unit, respectively, and f_i is the number of *H. dubius* stomachs containing prey items i in a unit. Based on these indices, the percentage of index of relative importance (%*IRI*)[42,43] was calculated for each prey item as follows:

$$IRI_i = (\%N_i + \%W_i) \times \%F_i$$

$$\%IRI_i = IRI_i \times 10^2 / \sum_{i=1}^{n} IRI_i$$

Because the body weight of *H. dubius* is approximately proportional to the third power of total length in both sexes,[31] Fulton's condition factor (*K*) was calculated to estimate the nutritive conditions. The feeding intensity was estimated from stomach contents index (*SCI*):

$$K = BW \times 10^5 / TL^3$$

$$SCI = SCW \times 10^2 / BW$$

where *TL* is the total length (mm), *BW* is the body weight (g) and *SCW* is the stomach contents weight (g). The *K* was calculated for the samples collected from late August to early September in each year. Gonads of male and female *H. dubius* during this period were approximately <1% of the body weight. The diet composition and feeding intensity were examined for the samples taken from the central part of the bay where hypoxia occurred in 1995–1997, and TL and K were examined for the samples from more extensive areas (Fig. 1). To compare the growths of each year-class the samples collected chiefly from late August to early September were used. Although in 1994 and 2001 the samples collected in early October and late October–early November were used, respectively, no correction was conducted.

One-way ANOVA was used to test for significant differences in TL and K among year-classes. When a significant difference was found among three year-classes, multiple comparisons were made between two year-classes by Scheffe's test. Temporal and spatial changes in prey abundance were determined through a two-way ANOVA. Prey abundance data were log-transformed [(log(x + 1)] prior to analysis.

RESULTS

The majority (89%) of 5697 *H. dubius* collected from 1993 to 2001 were composed of three year-classes (1989, 1991 and 1995). The mean TL values of the 1995 year-class were significantly smaller than those of the 1989 and 1991 year-classes at ages 2–6 in both sexes ($P < 0.01$ in all cases; Fig. 2). However, its difference was approximately constant after age 4. Conversely, the mean TL values at age 2 of the 1995 year-class were significantly larger than those of the 1991 year-class ($P < 0.05$ for male, $P < 0.001$ for female). The mean condition factors (K-value) of the 1995 year-class were significantly lower than those of the other two year-classes at ages 2–5 in both sexes ($P < 0.01$ in all cases; Fig. 3).

The diet compositions of *H. dubius* collected from August 2000 to May 2001 are shown in Fig. 4. The principal prey items of fish ≤200 mm TL were mysids (49–84%, almost all were *Neomysis czerniawskii*) in August, October and March, and ophiuroids (61%, almost all were *Ophiura sarsi*) in May. The diet composition of fish ≥201 mm TL varied among months, and the principal prey items were natant decapods (chiefly *Eualus macilenta*), fish (chiefly prickleback *Anisarchus macrops* and young walleye pollock *Theragra chalcogramma*), a bivalve *Portlandia japonica* and a pelagic amphipod *Themisto japonica*. The %*IRI* of fish and *P. japonica* tended to increase with the size of *H. dubius*. The *SCI* was very low from August 2000 to May 2001 in both sexes (median value: 0–0.23 for male, 0–0.17 for female; Fig. 5).

Figure 6 shows the horizontal distributions of *Ophiura* spp., *P. japonica and* natant decapods from June 2000 to May 2001. The abundance of

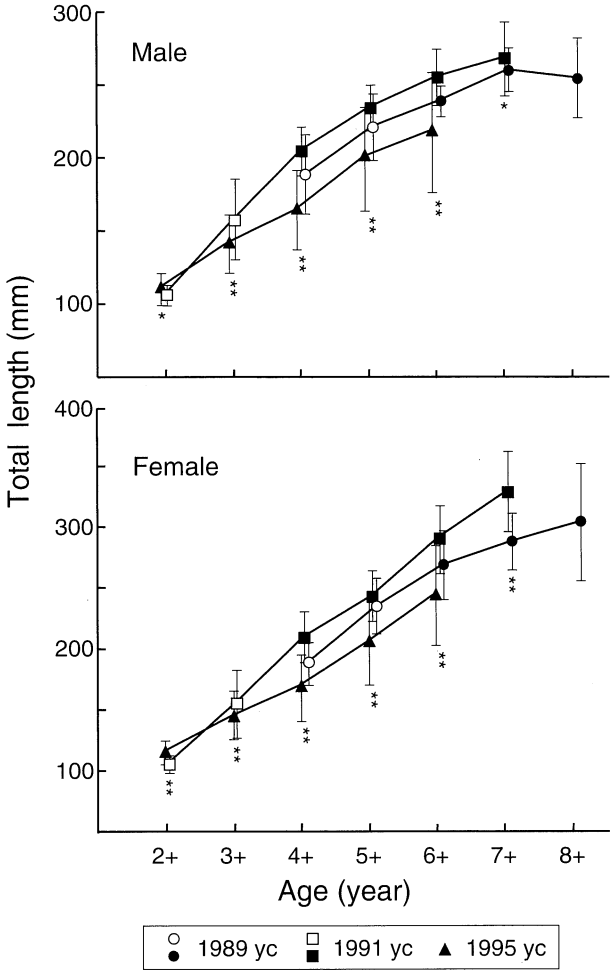

Fig. 2 Mean (±SD) total lengths at each age of the three year-classes (1989, 1991 and 1995) of *Hippoglossoides dubius*. Open and closed marks indicate before and after hypoxic event in 1995, respectively. $^{*}P < 0.05$; $^{**}P < 0.01$. Sample size for each data is ≥16.

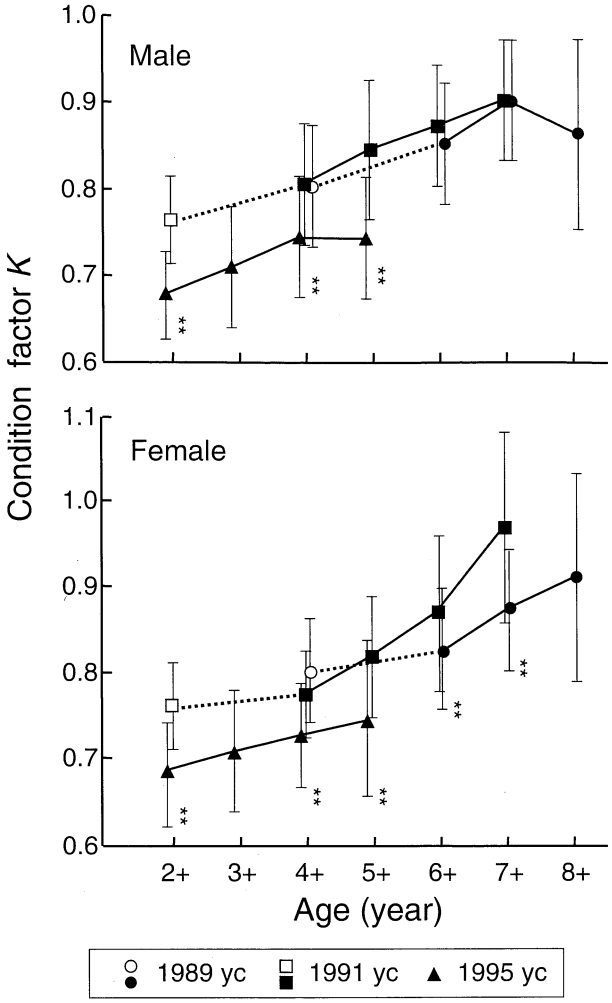

Fig. 3 Mean (±SD) condition factors at each age of the three year-classes (1989, 1991 and 1995) of *Hippoglossoides dubius*. Open and closed marks indicate before and after hypoxic event in 1995, respectively. $^{*}P < 0.05$; $^{**}P < 0.01$. Sample size for each data is ≥16.

Ophiura spp. was high off Mori (Stn 29 and nearby waters) and generally was low in the central part of the bay. The abundance of *Ophiura* spp. differed significantly by station ($P < 0.05$), while the differences among months was not significant ($P = 0.13$). The highest abundance was 621 individuals (ind.)/100 m^2 in June 2000, 1296 ind./100 m^2 in October–November 2000 and 1372 ind./100 m^2 in May 2001. In contrast, the abundance of *P. japonica* and natant decapods was not low in the central part of the bay. The abundance of *P. japonica* and natant decapods was not significantly different among stations ($P = 0.30$, $P = 0.41$) or months ($P = 0.69$, $P = 0.92$). The highest abundance of *P. japonica* was 55 ind./100 m^2 in June 2000, 84 ind./100 m^2 in October–November 2000 and 140 ind./100 m^2 in May 2001. The highest abundance of natant decapods was 68 ind./100 m^2 in June 2000, 67 ind./100 m^2 in October–November 2000 and 185 ind./100 m^2 in May 2001.

DISCUSSION

The abundance of *H. dubius* in Funka Bay fluctuates remarkably among year-classes, and in recent years three dominant year-classes (1989, 1991 and 1995) occurred.[36] Of these three year-classes, the fish born in 1995 when severe hypoxic water occurred were smallest in total length (Fig. 2) and lowest in condition factor (Fig. 3). The average size of American plaice *Hippoglossoides platessoides* in

Grand Bank became smaller when the fish abundance increased.[44] In the present study, however, the catch per unit effort (CPUE: the number of fish per 15-min tow) of *H. dubius* in 1993–2000 did not vary widely. Namely, the mean CPUE (±SD) in the central part of the bay and nearby waters from late August to early September was less variable, ranging from 126.8 ± 73.1 fish/tow in 1998 to 236.7 ± 208.4 fish/tow in 1993, except for 1995 (81.7 ± 126.1 fish/tow).[28] In addition, the total length at age 2 of the 1995 year-class was larger than that of the other year-class (1991; Fig. 2). From these facts, it cannot be considered that the tardy growth of the 1995 year-class is due to the high population density of *H. dubius*.

According to Yokoyama *et al.* the *H. dubius* in Funka Bay consumed chiefly ophiuroids, fish, mysids and natant decapods in 1985–1986. In particular, ophiuroids were the most important prey for both the small- (≤200 mm TL) and large-sized fish (>200 mm TL) through the year.[33,35] A similar situation was observed in 1982–1983.[45] However, *H. dubius* in 2000–2001 fed chiefly on mysids, fish, natant decapods, *T. japonica* and *P. japonica*, and the relative importance of ophiuroids was very low except for fish of ≤200 mm TL in May 2001 (Fig. 4; Table 2). In south-east Kattegat, Sweden, hypoxia changed the food supply for Atlantic cod and plaice *Pleuronectes platessa*, and their principal prey changed from crustaceans and molluscus to polychaetes and ophiuroids (chiefly *Amphiura filiformis*). This dietary shift decreased the nutritional value of the food taken and decreased the average size of fish.[21] It is known that *A. filiformis* have high tolerance to hypoxia.[46] In the present study the principal prey of *H. dubius* changed from ophiuroids (a low energy content)[35] to crustaceans and bivalves (a high energy content).[35,47] But the feeding intensity during the active feeding season (peak, May–July[31]) in 2000–2001 was low compared with that in the 1980s. Namely, the proportion of *H. dubius* having a low *SCI* (<0.5) from mid-May to August was approximately 50% in 1985–1988 (sampling time: 10:00–15:00),[31] while that in 2000–2001 were 65–77% for both sexes (Fig. 5). In addition, the mean SCI values in 2000–2001 (0.3–1.0, male; 0.8–0.9, female) were low as compared with those in 1985–1988 (0.5–0.9, male; 0.7–1.6, female).[31] Yokoyama reported that most of the *Ophiura* spp. consumed by *H. dubius* was ≤7 mm in disk dia-

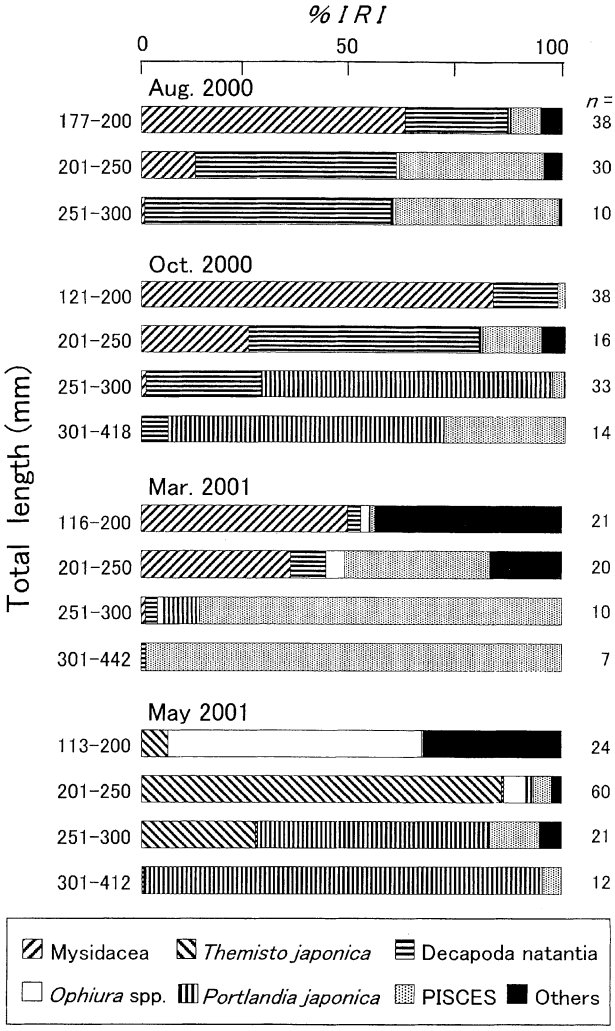

Fig. 4 Diet compositions of *Hippoglossoides dubius*, by size group of fish and month, expressed as percentage of index of relative importance (%*IRI*) for prey items. *n*, number of stomachs examined.

Table 2 Comparisons of principal food of *Hippoglossoides dubius* in Funka Bay between 1985–1986 (Yokoyama *et al.*[33]) and 2000–2001

Month	1985–1986	2000–2001
July–Aug.	*Ophiura* spp.	Mysidacea, Decapoda natantia and Pisces
Oct.–Nov.	*Ophiura* spp. and Pisces	Mysidacea, Decapoda natantia and *Portlandia japonica*
Feb.–Mar.	*Ophiura* spp., Mysidacea and Decapoda natantia	Mysidacea and Pisces
May	*Ophiura* spp. and Pisces	*Ophiura* spp., *Themisto japonica* and *Portlandia japonica*

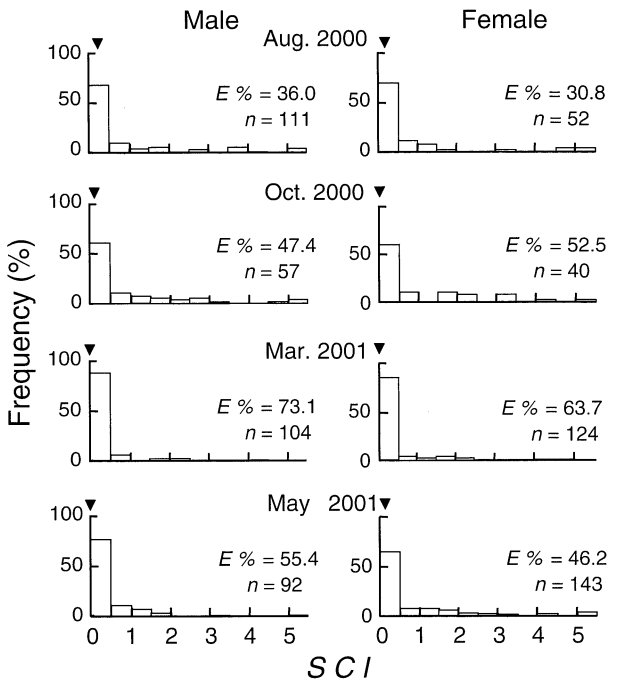

Fig. 5 Frequency distributions and medians (▼) of stomach contents index (*SCI*) of *Hippoglossoides dubius*. *E* %, percentage of empty stomachs; *n*, number of stomachs examined.

meter, and the abundance was high (>500 ind./100 m^2) at almost all of the stations (>50 m depth) in the bay through the year in 1985–1986.[35] Although the data of ophiuroids in 2000–2001 contained all individuals collected, the abundance was very low in the central part of the bay, especially in June 2000 (Fig. 6). Therefore, it seems probable that the main factor of tardy growth of the 1995 year-class is the poor food intake caused by the reduction of prey abundance, particularly ophiuroids.

From August to November, the main habitat of *H. dubius* is formed in areas deeper than 80 m (4–9°C) because of avoidance of high temperatures.[30] The CPUE of *H. dubius* in the deeper area (>90 m) during hypoxia was low compared with that in the shallower area, and this situation was remarkable in 1995.[28] Such a habitat shift to a high temperature area might have had an effect on the tardy growth of fish through the increase of the basal metabolism. However, it can be considered that the influence of water temperature was not large, judging from the facts that an apparent reduction in growth was not found in both the 1989 and 1991 year-classes after the hypoxic period (Fig. 2). This is probably related to the fact that the duration of shift to the shallower area was not long. For example, in mid-October 1995 the CPUE of *H. dubius* was not low in the central part of the bay and nearby waters (353.3 ± 150.1 fish/tow).[28]

The total length of the 1995 year-class was larger than that of the 1991 year-class at age 2 (Fig. 2), indicating that the feeding activity of 0–1-year-old fish was hardly influenced by the reduction of ophiuroids. The reason for this is that the 0–1-year-old *H. dubius* in the bay feeds on chiefly demersal plankton such as *Microcalanus pygmaeus* or mysids including *Archaeomysis* sp. (Kimura M, unpubl. data, 2003), and the majority of 0–1-year-old fish were not distributed in the central part of the bay and nearby waters.[28] The low condition factor at age 2 of the 1995 year-class (Fig. 3) is probably related to a dietary change from demersal plankton to benthos including ophiuroids in addition to habitat shift to the central part of the bay. As aforementioned, an apparent reduction of growth was not found in both the 1989 and 1991 year-classes after the hypoxic event in 1995. Although there is no available information on the diets of *H. dubius* in the 1990s, the majority of fish of the two aforementioned year-classes grew up to 200 mm TL or more at the hypoxic event (Fig. 2), and thereby probably consumed mainly fish such as young walleye pollock that were predominant in the bay.[48] Similarly, the reduction of growth was not found in the 1995 year-classes after age 5, although the condition factors were low (Figs 2,3). This indicates that the reduced abundance of benthic animals (chiefly ophiuroids) strongly affected the 2–4-year-old fish.

It is known that the abundances of ophiuroids and most of the crustaceans, gastropods and bivalves decrease drastically in hypoxic events. For example, in Amakusa-Tomoe Bay ophiuroids and sea urchin *Echinocardium cordatum* disappeared, and the number of species of bivalves and gastropods decreased.[17] Also, in Hiuchi Nada on the Seto Inland Sea, crustaceans such as gammarids decreased in the number of species and abundance.[16] A similar fact was also reported from Tokyo Bay: *Crangon affinis* and *Ophiura kinbergi* were not collected under oxygen concentration ≤1 mg/L (~0.7 mL/L).[20] Maita and Yanada reported that bottom water with oxygen concentration ≤2.0 mL/L did not occur in the bay from 1998 to 2001 (Table 3).[49–51] However, the abundance of ophiuroids was still low in 2000–2001, except for off Mori (Fig. 6). Most ophiuroids continue to grow for periods of 8 years at least, and probably for 10 or 15 years, and *O. sarsi* barely reach half their maximum size over a 2–4-year period.[52] It seems likely that the tardy recovery of ophiuroid abundance in the bay is related to their long life cycle.

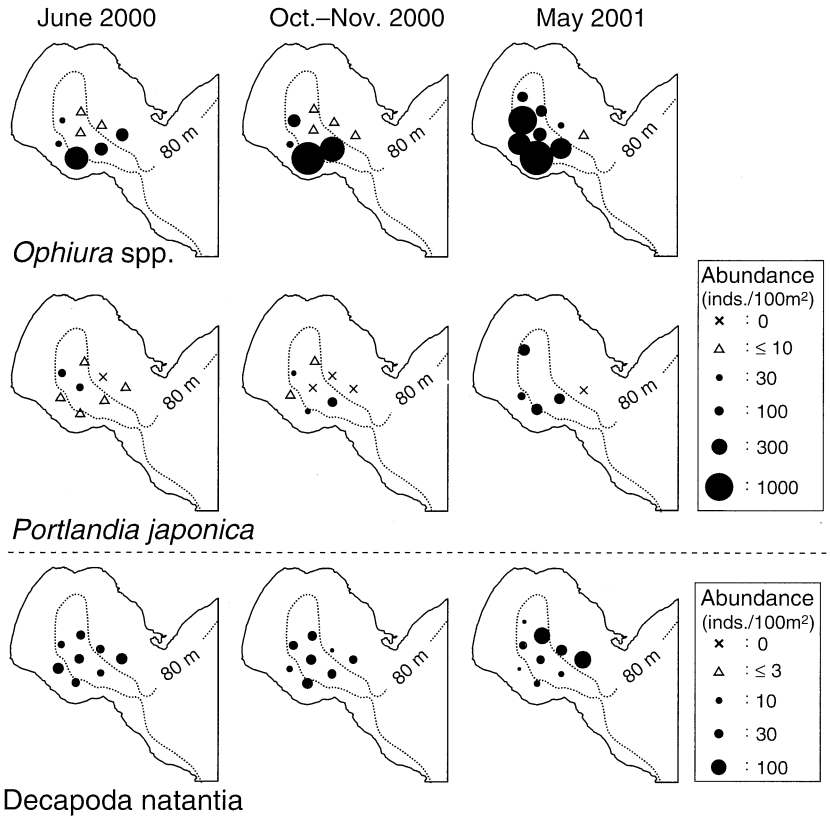

Fig. 6 Spacial distributions of *Ophiura* spp., *Portlandia japonica and* natant decapods collected with a sledge net.

Table 3 Dissolved oxygen concentration (DO) near the bottom in the central part of Funka Bay

Date	Station no.	DO (mL/L)†	Source
24 July 1995	30	0.58	Maita[49]
23 Aug. 1996	30	0.91	Maita[49]
4 Oct. 1997	30	1.07	Maita[50]
28 Aug. 1998	30	2.67	Maita[50]
29 Sep. 1999	30	3.29	Maita[50]
23 Aug. 2000	33	2.52	Present study
27 Aug. 2001	33	2.4	Yanada[51]

†Lowest values observed in each year are shown.

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REFERENCES

1. Diaz RJ, Rosenberg R. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol. Annu. Rev* 1995; **33**: 245–303.
2. Rossignol-Strick M. A marine anoxic event on the Brittany coast, July, 1982. *J. Coast. Res.* 1985; **1**: 11–20.
3. Gray JS, Wu RS, Or YY. Effects of hypoxia and organic enrichment on the coastal marine environment. *Mar. Ecol. Prog. Ser.* 2002; **238**: 249–279.
4. Vetter RAH, Franke HD, Buchholz F. Habitat-related differences in the response to oxygen deficiencies in *Idotea baltic* and *Idotea emarginata* (Isopoda, Crustacea). *J. Exp. Mar. Biol. Ecol.* 1999; **239**: 259–272.
5. Chabot D, Dutil J. Reduced growth of Atlantic cod in nonlethal hypoxic conditions. *J. Fish Biol.* 1999; **55**: 472–491.
6. Chew SF, Ip YK. Biochemical adaptations of the mudskipper *Boleophthalmus boddaerti* to a lack of oxygen. *Mar. Biol.* 1992; **112**: 567–571.
7. Low WP, Peng KW, Phuan SK, Lee CY, Ip YK. A comparative study on the responses of the gills of two mudskippers to hypoxia and anoxia. *J. Comp. Phisiol. B* 1993; **163**: 487–494.
8. via Dalla J, van den Thillart G, Cattani O, de Zwaan A. Influence of long-term hypoxia exposure on the energy metabolism of *Solea solea.* II. Intermediary metabolism in blood, liver and muscle. *Mar. Ecol. Prog. Ser.* 1994; **111**: 17–27.
9. via Dalla J, van den Thillart G, Cattani O, Cortesi P. Environmental versus functional hypoxia/anoxia in sole *Solea solea*: the lactate paradox revisited. *Mar. Ecol. Prog. Ser.* 1997; **154**: 79–90.
10. Nilsson HC, Skold M. Arm regeneration and spawning in the brittle star *Amphiura filiformis* (Müller OF) during hypoxia. *J. Exp. Mar. Biol. Ecol.* 1996; **199**: 193–206.

11. Nilsson HC. Effects of hypoxia and organic enrichment on growth of the brittle star *Amphiura filiformis* (Müller OF) and *Amphiura chiajei* Forbes. *J. Exp. Mar. Biol. Ecol.* 1999; **237**: 11–30.
12. Baker MS, Mann R. Description of metamorphic phases in the oyster *Crassostrea virginica* and effects of hypoxia on metamorphosis. *Mar. Ecol. Prog. Ser.* 1994; **104**: 91–99.
13. Wang WX, Widdows J. Physiological responses of mussel larvae *Mytilus edulis* to environmental hypoxia and anoxia. *Mar. Ecol. Prog. Ser.* 1991; **70**: 223–236.
14. Rosas C, Martinez E, Gaxiola G, Brito R, Sanchez A, Soto LA. The effect of dissolved oxygen and salinity on oxygen consumption, ammonia excretion and osmotic pressure of *Penaeus setiferus* (Linnaeus) juveniles. *J. Exp. Mar. Biol. Ecol.* 1999; **234**: 41–57.
15. Forbes TL, Lopez GR. The effect of food concentration, body size, and environmental oxygen tension on the growth of the deposit-feeding polychaete, *Capitella* species 1. *Limnol. Oceanogr.* 1990; **35**: 1535–1544.
16. Imabayashi H. Effects of oxygen-deficient water on the benthic communities. *Nippon Suisan Gakkaishi* 1983; **49**: 7–15.
17. Kikuchi T. Eutrophication in the sea area and indicators of benthic animals. In: The Japanese Society of Scientific Fisheries (ed.). *Eutrophication and Biological Indicators in Coastal Waters.* Kouseisha Kouseikaku, Tokyo. 1982; 84–100.
18. Pearson TH, Josefson AB, Rosenberg R. Petersen's stations revisited. I. Is the Kattegat becoming eutrophic? *J. Exp. Mar. Biol. Ecol.* 1985; **92**: 157–206.
19. Josefson AB, Widbom B. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Mar. Biol.* 1988; **100**: 31–40.
20. Furota T. Survival and population maintenance of macrobenthic animals in inner Tokyo Bay. *Bull. Coast. Oceanogr.* 1991; **28**: 160–169.
21. Pihl L. Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. *Can. J. Fish. Aquat. Sci.* 1994; **51**: 321–336.
22. Pihl L, Baden SP, Diaz RJ. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Mar. Biol.* 1991; **108**: 349–360.
23. Pihl L, Baden SP, Diaz RJ, Schaffher LC. Hypoxia-induced structural changes in the diet of bottom-feeding fish and crustacea. *Mar. Biol.* 1992; **112**: 349–361.
24. Baden SP, Loo L-O, Pihl L, Rosenberg R. Effects of eutrophication on benthic communities including fish: Swedish west coast. *Ambio* 1990; **19**: 113–122.
25. Maita Y. The ecosystem and behavior of the nutrient element in Funka Bay, Hokkaido. *Bull. Jpn. Soc. Fish. Oceanogr.* 1980; **37**: 33–36.
26. Maita Y, Yanada M. Funka Bay III Chemistry. In: Coastal Oceanography Research Committee, The Oceanographical Society of Japan (ed.). *Coastal Oceanography of Japanese Islands.* Tokai University Press, Tokyo. 1985; 113–125.
27. Maita Y. [On the hypoxic events during summer in Funka Bay, Hokkaido]. *Suisan Gakujutsu Kenkyuu Kairyou Hojo Jigyou Houkoku* (Annual Report of Fisheries Study published by The Hokusui Society Foundation). The Hokusui Society Foundation, Sapporo. 1998; 31–44 (in Japanese).
28. Maeda T, Nakatani T, Takatsu T. [Studies on oceanographic conditions, and distribution and fluctuation in stocks of flathead flounder Hippoglossoides dubius and coonstripe shrimp Pandalus hypsinotus in Funka Bay, Hokkaido.] *Suisan Gakujutsu Kenkyuu Kairyou Hojo Jigyou Houkoku.* The Hokusui Society Foundation, Sapporo. 2001; 37–57 (in Japanese).
29. Hayashi K. *Hippoglossoides dubius* in Funka Bay, Hokkaido. *J. Hokkaido Fish. Exp. Stn* 1963; **20**: 6–15.
30. Yokoyama S, Maeda T, Nakatani T, Takahashi T, Matsushima H. Distribution and migration of *Hippoglossoides dubius* in Funka Bay and its offshore waters, Hokkaido. *Bull. Jpn. Soc. Fish. Oceanogr.* 1990; **54**: 373–380.
31. Yokoyama S, Maeda T, Takahashi T, Nakatani T, Matsushima H. Annual life cycle of adult *Hippoglossoides dubius* in Funka Bay, Hokkaido. *Nippon Suisan Gakkaishi* 1991; **57**: 1469–1476.
32. Hayase H, Hamai I. Studies on feeding habits of three flatfishes, *Cleisthenes pinetorum herzensteini* (Schmidt), *Hippoglossoides dubius* (Schmidt) and *Glyptocephalus stelleri* (Schmidt). *Bull. Fac. Hokkaido Univ.* 1974; **25**: 82–99.
33. Yokoyama S, Maeda T, Nakatani T. Diet composition of *Hippoglossoides dubius* and distribution of megalobenthos in Funka Bay and its offshore waters, Hokkaido. *Nippon Suisan Gakkaishi* 1994; **60**: 719–726.
34. Nakatani T, Koizumi H, Yokoyama S, Maeda T, Takahashi T, Matsushima H. Age and growth of Pleuronectid flounder *Hippoglossoides dubius* in Funka Bay, Hokkaido. *Nippon Suisan Gakkaishi* 1990; **56**: 893–901.
35. Yokoyama S. Ecological study on distribution and feeding of *Hippoglossoides dubius* in Funka Bay and its offshore waters, Hokkaido. PhD Thesis. Hokkaido University, Hakodate, 1992.
36. Nakatani T, Maeda T, Sugimoto K, Takatsu T, Takahashi T. Possible causes of annual change in the year class strength of flathead flounder *Hippoglossoides dubius* (Pisces, Pleuronectiformes) in Funka Bay, Hokkaido. *Bull. Jpn. Soc. Fish. Oceanogr.* 2002; **66**: 216–223.
37. Ohtani K, Akiba Y. Studies on the change of hydrographic conditions in the Funka Bay I. The annual change of the water of the bay. *Bull. Fac. Fish. Hokkaido Univ.* 1970; **20**: 303–312.
38. Ohtani K. Studies on the change of hydrographic conditions in the Funka Bay II. Characteristics of the waters occupying the Funka Bay. *Bull. Fac. Fish. Hokkaido Univ.* 1971; **22**: 58–66.
39. Ohtani K, Kido K. Oceanographic structure in Funka Bay. *Mem. Fac. Fish. Hokkaido Univ.* 1980; **31**: 84–114.
40. Ohshima K, Yokota S. Oceanographic description of the coast of Japan XXV. Funka Bay (IV): geology and geography. *Bull. Coast. Oceanogr.* 1983; **20**: 189–203.
41. Maita Y, Nakao S. Studies on environmental conditions of cultivated scallop *Patinopecten yessoensis* in Funka Bay, Hokkaido. *Suisan Gakujutsu Kenkyuu Kairyou Hojo Jigyou Houkoku* (Annual Report of Fisheries Study published by The Hokusui Society Foundation). The Hokusui Society Foundation, Sapporo. 1996; 17–25 (in Japanese).
42. Pinkas L, Oliphant MS, Iverson ILK. Food habits of albacore, bluefin tuna and bonito in California waters. *Fish. Bull.* 1971; **152**: 1–105.
43. Cortés E. A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* 1997; **54**: 726–738.
44. Pitt TK. Changes in abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglos-*

soides platessoides. J. Fish. Res. Board Can 1975; **32**: 1383–1398.
45. Yokoyama S. Studies on distribution of benthic animals and food habits of *Hippoglossoides dubius* Schmidt and *Glyptocephalus Stelleri* (Schmidt) in Funka Bay and adjacent waters, Hokkaido. MS Thesis, Hokkaido University, Hakodate, 1985.
46. Vistisen B, Vismann B. Tolerance to low oxygen and sulfide in *Amphiura filiformis* and *Ophiura albida* (Echinodermata: Ophiuroidea). *Mar. Biol.* 1997; **128**: 241–246.
47. Brey T, Rumohr H, Ankar S. Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *J. Exp. Mar. Biol. Ecol.* 1988; **117**: 271–278.
48. Yokoyama S, Maeda T, Takahashi T, Nakatani T, Matushima H. Temporal and spatial distributions of demersal fish in Funka Bay and offshore, Hokkaido. *Mem. Fac. Fish. Hokkaido Univ.* 1989; **40**: 8–21.
49. Maita Y. Time series changes of dissolved oxygen and lipid composition in bottom sediments in Funka Bay, Hokkaido. *Suisan Gakujutsu Kenkyuu Kairyou Hojo Jigyou Houkoku* (Annual Report of Fisheries Study published by The Hokusui Society Foundation). The Hokusui Society Foundation, Sapporo. 1997; 19–26 (in Japanese).
50. Maita Y. Studies on sinking particles and sediments for clarifying the origin of hypoxia in Funka Bay, Hokkaido. *Suisan Gakujutsu Kenkyuu Kairyou Hojo Jigyou Houkoku* (Annual Report of Fisheries Study published by The Hokusui Society Foundation). The Hokusui Society Foundation, Sapporo. 2000; 34–45 (in Japanese).
51. Yanada M. Contribution of accumulation process of organic matters to hypoxia in bottom water in Funka Bay, Hokkaido. *Suisan Gakujutsu Kenkyuu Kairyou Hojo Jigyou Houkoku* (Annual Report of Fisheries Study published by The Hokusui Society Foundation). The Hokusui Society Foundation, Sapporo. 2002, 3–10 (in Japanese).
52. Fell HB. The ecology of ophiuroids. In: Boolootian RA (ed). *Physiology of Echinodermata.* Interscience Publishers, New York. 1966; 129–143.