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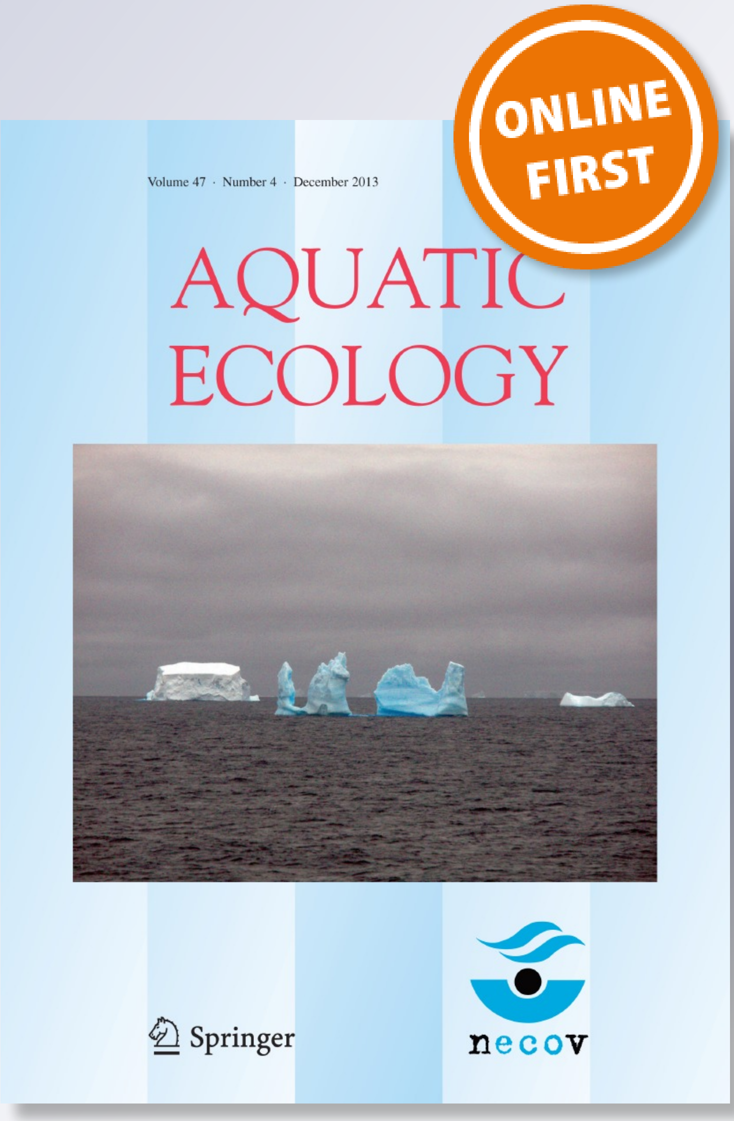

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Upwelling-like bottom intrusion enhances the pelagic–benthic coupling by a fish predator in a coastal food web

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Abstract Upwelling regions where nutrients are transported from deep to surface waters are among the most productive in the oceans. Although it is well known that the upwelling affects fishery production through bottom-up trophic cascading, it remains unexplored how temporal variation in its intensity alters overall trophic energy flows within a focal food web. In the present study, we demonstrate that inter-annual variation in the intensity of upwelling-like bottom intrusion alters food web properties in coastal waters of the Uwa Sea by focusing on the levels of δ^{13}C and δ^{15}N for a demersal fish predator, *Acropoma japonicum*. This approach integrates information on prey–predator interactions. In the season following a stratification period when pelagic productivity is limited by nutrient availability, *A. japonicum* showed lower levels of δ^{13}C in years with high bottom intrusion intensity than in those with low intensity. One possible cause for this isotopic depletion is that the bottom intrusion-induced nutrient supply enhances pelagic productivity and consequently facilitates a foraging shift by *A. japonicum* from ordinary benthic prey to supplementary pelagic prey with a lower δ^{13}C. In conclusion, the increased intensity of bottom intrusion results in coupling of two major trophic energy flows, pelagic and benthic food chains, through the demersal predator's foraging shift.

Keywords Bottom-up trophic cascade · Coastal upwelling · Food webs · Pelagic–benthic coupling · Stable isotope analysis

Introduction

In pelagic ecosystems in which nutrients are prone to depletion, oceanophysical processes play an important role in determining ecosystem properties, such as primary productivity and trophic energy flows (Mann 1993). Upwelling, which is driven by physical forces, such as winds, Coriolis effects, and Ekman transport, transports a huge quantity of nutrients from deep to surface waters, enhancing plankton growth and consequently fish production (Bakun 1990; Mann 2000).

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It also affects the feeding habits, biomass, and distribution of top predators such as fish and seabirds through the bottom-up trophic cascading effects, altering trophic energy flows within the coastal ecosystem (Brodeur and Pearcy 1992; Ainley et al. 1996; Ware and Thomson 2005; Thompson et al. 2012). Upwelling takes place in limited regions of the world's oceans, and these regions are the most productive (Pauly and Christensen 1995).

Off the southern coasts of the Japanese archipelago, it is well known that cool nutrient-rich waters are sometimes transported from the continental slope to the coastal areas (Sugimoto et al. 2009). Previous studies have reported that advection of deep waters frequently occurs in the Bungo Channel. This upwelling-like phenomenon called "bottom intrusion" was mainly observed at neap tidal period from early summer to late autumn (Kaneda et al. 2002). The generation mechanism is different from that of the upwelling in other coastal seas, i.e., the bottom intrusion is not triggered by wind but by meanderings of offshore ocean current (Fig. 1). Based on a numerical study, it was suggested that the propagation of the small meander of the Kuroshio Current is related to the generation of the bottom intrusion (Arai 2005), although the mechanisms for the generation are not clear from the observational study. It also occurs sporadically but repeatedly through the year (Kaneda et al. 2002). In this region, the bottom intrusion accounts for a large proportion of nutrient pools in coastal waters and its frequent occurrence enhances pelagic productivity, especially during summer stratification period when nutrients are depleted. The temporal dynamics of bottom intrusion affects not only primary productivity but also secondary production (Nakano et al. 2004).

Although bottom intrusion is unique in its underlying mechanisms, it has the same ecosystem consequence as that of the upwelling, i.e., high ecosystem productivity, as demonstrated by the fact that the bottom intrusion areas are good fishery grounds (Hayami et al. 2006). Although many researchers have documented that the upwelling increases fishery production through bottom-up trophic cascading effects, it remains unexplored how temporal variation in its intensity influences overall trophic energy flows within a focal food web (Chavez and Messie 2009).

Stable isotope analysis, which has been considered a powerful tool for food web studies (Fry 2006), is a promising approach for the examination of the bottom-up effect on food web properties. In general, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios, expressed as the per mill deviation of heavy (^{13}C or ^{15}N) to light (^{12}C or ^{14}N) isotope ratio from that of standards, are used to characterize trophic pathways of aquatic food webs. On the one hand, the $\delta^{13}C$ changes little through trophic interactions and hence helps to either indicate the source of energy leading to consumers or the relative important of multiple trophic pathways leading to consumers (DeNiro and Epstein

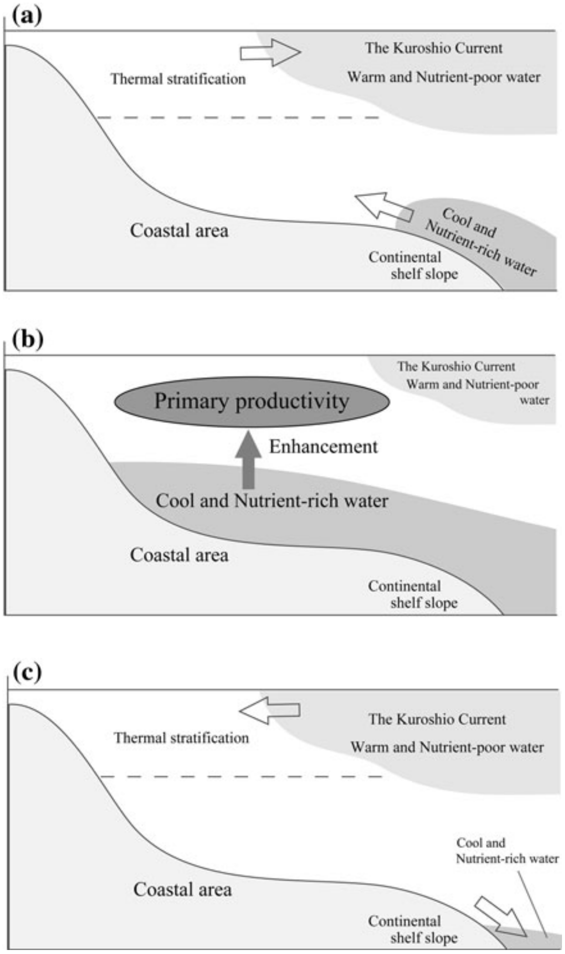

Fig. 1 A schematic diagram of appearance and disappearance of bottom intrusion during summer stratification period. The *white arrow* indicates the movement of the water mass. **a** Cool and nutrient-rich water is transported from the continental shelf to coastal areas, driven by a small meander of the Kuroshio Current. **b** This water mass enhances primary productivity in pelagic waters with temporary disturbance of thermal stratification. **c** Thermal stratification is redeveloped after disappearance of the bottom intrusion

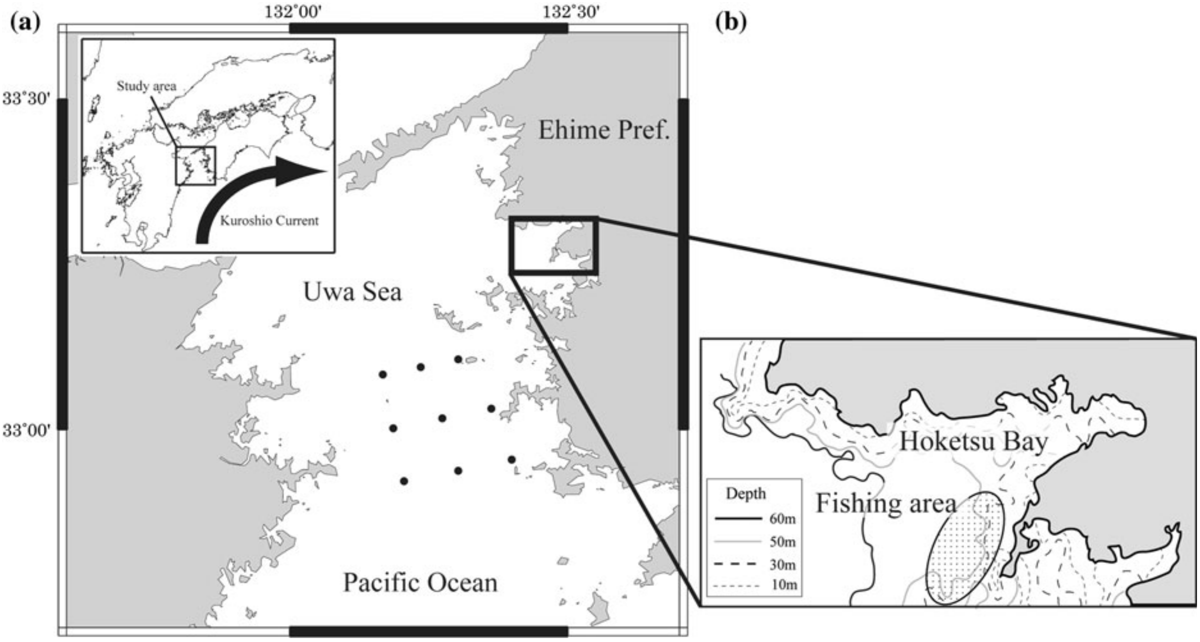

Fig. 2 Map of the study area in the Uwa Sea, southern Japan. The locations of oceanophysical monitoring sites (*black dots*) (**a**) and the local trawl fishing ground (*dotted area*) (**b**) are shown

1978). In coastal food webs in which phytoplankton and benthic microalgae are dominant primary producers, two trophic energy pathways, pelagic and benthic food chains, can be easily discriminated in terms of their carbon isotopic signatures because the $\delta^{13}C$ values of benthic microalgae are much higher than those of phytoplankton (France 1995). Taking the advantage of this isotopic traceability, it is possible to estimate to what extent consumers rely on a particular food chain based on the $\delta^{13}C$ of themselves and their basal resources. On the other hand, the $\delta^{15}N$ values regularly increase from lower to higher trophic levels (3.4 ‰ per trophic level), and hence serves as an indicator of consumers' trophic levels (Minagawa and Wada 1984). With the development of isotope mixing models, this technique has now been established as a standard and quantitative method for food web analysis (Post 2002).

Using stable isotope analysis, we aim to examine how the intensity of upwelling-like bottom intrusion affects food web properties in coastal waters of the Uwa Sea (Fig. 2a), which are under the strong influence of the Kuroshio Current. To integrate information on trophic interactions in the coastal food web of this sea, we focus on the extent to which inter-annual variation in the bottom intrusion intensity (BII) alters the $\delta^{13}C$ and $\delta^{15}N$ for *Acropoma japonicum*, which is a dominant predator of demersal communities (Okuda et al. 2005). After settling at the bottom as juveniles in late summer, the fish shift their food habits from small zooplankton to large zoobenthos, such as shrimps and benthic fish juveniles, thereby showing the ontogenetic niche shift indicated by their isotopic signatures (Hamaoka et al. 2010a). However, the fish always have access to both pelagic and benthic prey through a vertical feeding migration in the night. Since the fish could feed in either habitat, it is possible that they prefer one over the other where prey availability is lower. Through such a feeding behavior, adult fish flexibly and drastically switch toward pelagic prey, such as copepods and larval anchovy, during spring algal blooms. Thereafter, they gradually return to feeding on the zoobenthos throughout the summer stratification period when pelagic productivity decreases due to nutrient depletion.

In this study, we test how the intensity of bottom intrusion affects trophic energy flows leading to the dominant predator *A. japonicum* through the bottom-up trophic cascading effect, assuming that the dominant predator's stable isotopic signatures reflect the proportion of individual mass that relied on pelagic production. For this fish, the reliance on pelagic production is estimated at an average of 21 % annually based on an isotope mixing model (Hamaoka et al. 2010a). However, the reliance also showed marked seasonal changes in response to the availability of pelagic prey, ranging from 34.3 % in the season following spring algal blooms to 7.8 % in the season following the summer stratification period (Hamaoka et al. 2010a).

Here, we put forward the following working hypothesis regarding the predator's response to the BII. During the summer stratification period, when pelagic waters are nutrient-depleted, the pelagic productivity will be enhanced by nutrient supply from the bottom intrusion. Consequently, *A. japonicum* will be supplemented with pelagic prey through the bottom-up trophic cascade, resulting in its stronger reliance on pelagic production than in times that with no or weak bottom intrusion. According to this hypothesis, we make a specific prediction that the δ^{13}C value of *A. japonicum* will decrease in years when the BII is high because *A. japonicum* feeds more on pelagic prey with a lower δ^{13}C value. Such a bottom intrusion-induced foraging shift will also result in a decrease in the δ^{15}N value for *A. japonicum* because small pelagic prey, such as crustacean zooplankton, have lower trophic levels than large zoobenthos prey (Hamaoka et al. 2010a). Although benthic macroalgal- and terrestrial-derived particulate organic matter are the potential basal resources, we assume that they have only a negligible effect on the isotopic signatures of *A. japonicum* because of their small contribution to the coastal food web in the Uwa Sea (Hamaoka et al. 2010a).

To test our hypothesis, we examine to what extent inter-annual variation in the BII alters δ^{13}C and δ^{15}N for *A. japonicum*, using 6 years of monitoring data.

Materials and methods

Subject species and sampling design

Acropoma japonicum shows some restricted distributions in coastal waters of southern Japan, which is under the strong influence of the Kuroshio Current (Hamaoka et al. 2010b). In our study area, the Uwa Sea, it inhabits the sandy bottom at an average depth of 70 m (Okuda et al. 2005). In the Uwa Sea, *A. japonicum* is regarded as a commercially important fishery resource because of its high biomass and area-specific rarity. This fish reproduces from June to September, and its hatched larvae live a planktonic life until they grow up to approximately 5 mm during the summer season (Konishi 1988). For the stable isotope analysis, we collected specimens of sub- and adult *A. japonicum* from Hoketsu Bay located in the northern part of the Uwa Sea (Fig. 2b), using a local fishing gear "Buri trawl" towed along the sandy bottom at a depth of ca. 60 m within 1 km of the shore line (Okuda et al. 2005). The sample collections were conducted each November from 2002 to 2007. November is the month that immediately follows the summer stratification period (May–October). Assuming that the body tissue turn-over takes a few months for this fish (Hamaoka et al. 2010a), stable isotope signatures of specimens collected in November would provide time-integrated information on their diets during the summer stratification period. In each year, we selected 20 fish whose total length had been measured (mm), such that our sample represented a nearly uniform coverage of the body size range of each sampling.

Stable isotope analysis

Prior to the stable isotope analysis, we excised muscle tissues from the dorsal portion of the lateral body and dried them at 60 °C for 24 h. The samples were then pulverized into a fine powder and immersed in a 2:1 chloroform/methanol solution for 24 h to remove lipids. After the lipid extraction, all samples were dried again at 60 °C for 24 h. Finally, they were wrapped with a tin capsule to measure their carbon and nitrogen stable isotope ratios using a mass spectrometer (ANCA-GSL, Sercon Inc., UK).

The carbon and nitrogen stable isotope ratios are expressed in δ notation and defined as the per mill deviation from the standard, as follows.

$$\delta^{13}\text{C or } \delta^{15}\text{N}(‰) = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000 \quad (1)$$

where R is ^{13}C/^{12}C or ^{15}N/^{14}N. The standards were Pee Dee belemnite (PDB) limestone carbonate for δ^{13}C and atmospheric nitrogen (N_2) for δ^{15}N. Analytical precision was 0.1 ‰ for δ^{13}C and 0.2 ‰ for δ^{15}N.

Bottom intrusion intensity

In the Uwa Sea, the bottom intrusions occur sporadically during the stratification period. Their summer occurrences can be easily detected by anomalies in the bottom water temperature. As the bottom intrusion-derived deep waters are much cooler than coastal waters, we defined BII as the deviation from the long-term average of the bottom water temperature in coastal areas (Kaneda et al. 2002). The long-term data on water temperature, which were provided by the Fisheries Research Center, Ehime Research Institute of Agriculture, Forestry and Fisheries, Ehime Prefecture, were taken from nine monitoring sites throughout the Uwa Sea to assess the intensity of bottom intrusion occurring on a regional scale (Fig. 2a).

To separate the effect of allochthonous nutrient input (i.e., derived from the continental slope) from that of autochthonous nutrient input (i.e., derived from the bottom of coastal areas due to vertical mixing), the BII was calculated only during summer stratification period (May–October) as follows:

$$\mathrm{BII} = T_{A75} - T_{S75} \tag{2}$$

where T_{A75} is the long-term average of bottom water temperature at a depth of 75 m in the Uwa Sea between May and October, from 1972 to 2008, and T_{S75} is the monthly average of bottom water temperature during the same period of each year of the study. A high positive value of BII indicates the high frequency and magnitude of bottom intrusions.

Data analysis

We tested to what extent six yearly cycles of variation in both δ^{13}C and δ^{15}N of *A. japonicum* can be accounted for by the variation in BII. Our previous study reported that *A. japonicum* shows a size-specific pattern in its δ^{13}C and δ^{15}N (Hamaoka et al. 2010a). In the present study, we also found significant correlations between its body size and isotopic signatures from our 6-year dataset (see "Results"). Therefore, δ^{13}C and δ^{15}N of individual fish should be corrected for their body size in order to separate the effects of inter-annual variation in the body size distribution from the effect of the BII on its isotopic signatures.

In order to examine the predator's isotopic responses to the BII, we performed a linear mixed model (LMM), incorporating the δ^{13}C or δ^{15}N of *A. japonicum* as response variables, its body size and the BII as covariates, and study years as a random factor into the models. For the data analysis, we used the statistical software package, SPSS version 16.0 (SPSS Inc., Chicago, IL, USA).

Results

When pooling data from all years, both the δ^{13}C and δ^{15}N of *Acropoma japonicum* showed size-specific patterns (Fig. 3). The δ^{15}N showed a significantly positive correlation with body size ($n = 120$, $r = 0.47$, $p < 0.0001$), indicating that the trophic level of *A. japonicum* increases with its body size. In contrast, the δ^{13}C showed a negative correlation with body size ($n = 120$, $r = -0.42$, $p < 0.0001$), indicating that the fish rely more on pelagic prey with increasing body size.

During the summer stratification period, the BII showed great inter-annual variation with the lowest value in 2004 and the highest in 2005 (Fig. 4). The LMM revealed that size-adjusted δ^{13}C value of *A. japonicum* tended to decrease in years with a higher BII, suggesting that the fish showed stronger reliance on pelagic production with increasing BII during the summer stratification period (Fig. 5; Table 1). Similar to the result of δ^{13}C, *A. japonicum* showed a marginal tendency to have a lower value of size-adjusted δ^{15}N in years when the BII was stronger (Fig. 5; Table 1).

Discussion

Bottom intrusion-induced trophic cascade

Using the 6 years of monitoring data, the stable isotope analysis for a predatory fish, *Acropoma japonicum*, revealed that its δ^{13}C value decreased in years with greater intensity of bottom intrusion. This result is consistent with the prediction that *A. japonicum* will rely more on pelagic energy flow when the pelagic production is enhanced by the bottom intrusion, especially under the nutrient-limited conditions during the summer stratification period. One possible mechanism for the inter-annual variation in its isotopic signatures is that *A. japonicum* shifted its feeding habit from ordinary benthic prey with a higher δ^{13}C to supplementary pelagic prey with a lower δ^{13}C in response to the relative abundance of two trophic energy flows derived from phytoplankton and benthic microalgae. Although many researchers have

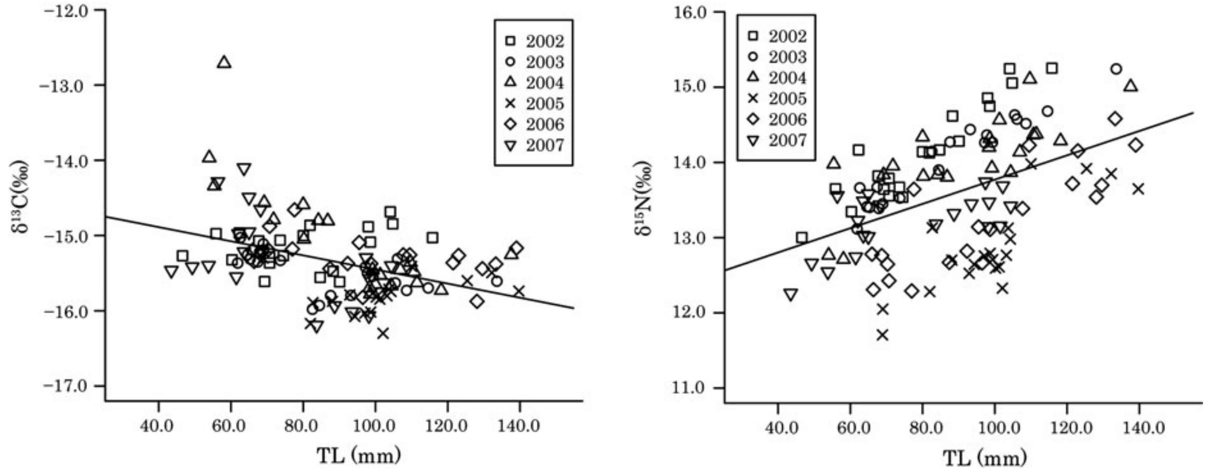

Fig. 3 The size-specific pattern of δ^{13}C (*left*) or δ^{15}N (*right*) for *A. japonicum*

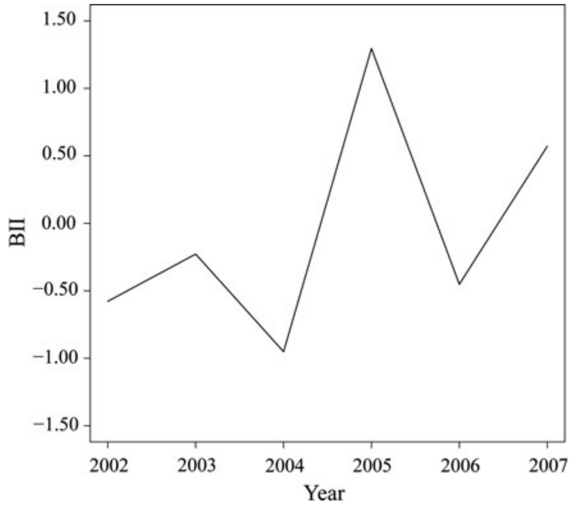

Fig. 4 Inter-annual variations in the BII during the summer stratification period

documented that fish production is higher in the upwelling areas than in the non-upwelling areas (Miller et al. 2010; Pikitch et al. 2012) or in the upwelling season than in the non-upwelling season (Ware and Thomson 1991), this study is the first to explore how the intensity of upwelling-like bottom intrusion influences overall trophic energy flows within a focal food web.

One may expect that the predators' isotopic variation is due to temporal variation in the basal isotopic signatures rather than to changes in their production reliance. If this were the case, it would be predicted that *A. japonicum* has a higher δ^{13}C value because phytoplankton δ^{13}C increases under a high growth condition (Laws et al. 1997), which is contrary to our observations. In general, temporal variation in the phytoplankton δ^{13}C is much smaller than the isotopic difference between pelagic and benthic food chains, suggesting that the δ^{13}C of *A. japonicum* strongly reflected its foraging shift to pelagic prey.

A. japonicum also tended to decrease its δ^{15}N value in years with greater BII, although the tendency was not statistically significant. One possible cause of this isotopic depletion is that the fish relied more on pelagic prey at lower trophic levels, such as crustacean zooplankton, than on benthic prey at higher trophic levels, such as decapods and fishes (Hamaoka et al. 2010a). In coastal waters of the Uwa Sea, Nakano et al. (2004) found that a trophic flow from phytoplankton to grazing zooplankton was enhanced quickly after the occurrence of bottom intrusions. The similar was also reported in a northern California Current with the upwelling system, in which fish predators have a lower δ^{15}N value in the area where upwelling is observed, suggesting that they feed more on pelagic prey at lower trophic levels (Miller et al. 2010).

Another mechanism to explain the predator's nitrogen isotopic response to the bottom intrusions may operate in the opposite direction. The bottom intrusion-induced nutrient transportation can alter the baseline of δ^{15}N in the coastal food webs because the δ^{15}N of primary producers reflects that of inorganic nitrogen derived from deep waters. In the Kuroshio Current, the nitrates of offshore waters have 2 ‰ more enriched ^{15}N than those of coastal waters

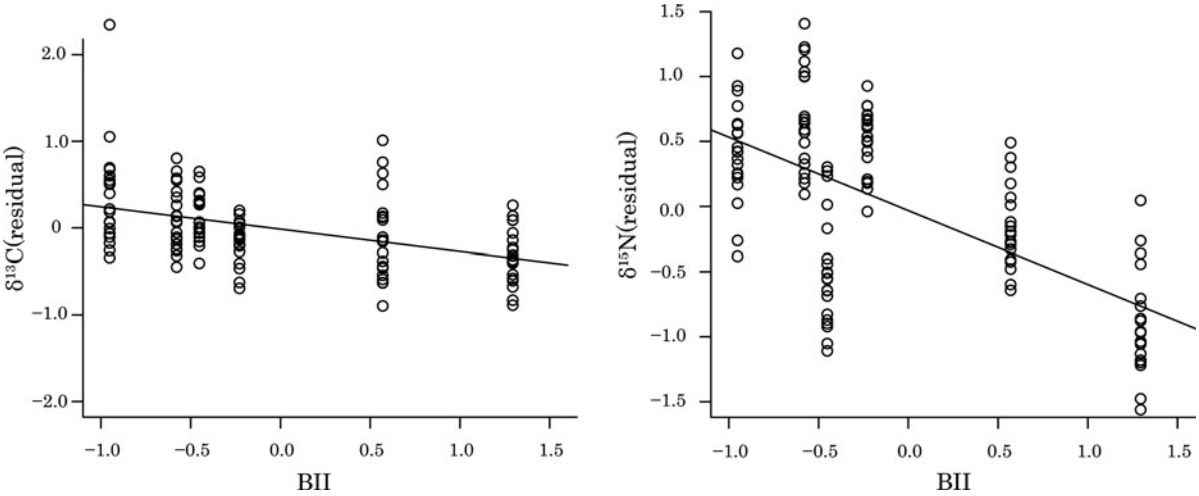

Fig. 5 Relationships between the BII and size-adjusted $\delta^{13}C$ or $\delta^{15}N$ of *A. japonicum* during the summer stratification period. *Solid lines* represent the regression lines drawn from the LMM (see Table 1)

Table 1 The results of the LMM examining the effects of BII on size-adjusted $\delta^{13}C$ and $\delta^{15}N$ of *A. japonicum*

	Coefficient	Intercept	df1	df2	F	N_{year}	$N_{\mathrm{observation}}$	p
$\delta^{15}N$	−0.57	−0.033	1	4	5.04	6	120	0.088
$\delta^{13}C$	−0.26	−0.01	1	4	14.3	6	120	0.019

(Sugimoto et al. 2009, 2010). According to this oceanogeochemical pattern, it is predicted that coastal phytoplankton will have a higher $\delta^{15}N$ in years with higher BII, by assimilating the ^{15}N-enriched nutrients of Kuroshio-derived deep waters. Such an isotopic signal may be trophically cascaded up to the predators. If this is true, the baseline effect may be offset by the effect of decreased predator trophic levels through the foraging shift to pelagic prey, resulting in the unclear effect of BII on the $\delta^{15}N$ of *A. japonicum*. At present, we have technical difficulties in discriminating between trophic and basal effects on the basis of $\delta^{15}N$ data and need another natural tracer to detect coastal and pelagic water-derived nutrients.

Pelagic–benthic coupling by fish predators

In the present study, we found that the $\delta^{13}C$ of *A. japonicum* is negatively correlated with its body size, suggesting that larger fish show a higher reliance on pelagic production. This result seems to be counterintuitive when considering that the fish show an ontogenetic foraging shift from small pelagic prey to large benthic prey (Hamaoka et al. 2010a). In general, larger predators, which have higher mobility and a larger gape size, can select a wider range of prey depending on their body size relative to prey and on prey availability (Briones et al. 2012). In the case of *A. japonicum*, larger fish might prefer to feed not only on large benthic prey, but also on large pelagic prey at higher trophic levels (e.g., anchovy and krill) through their vertical migration (Hamaoka et al. 2010a). Since *A. japonicum* is a demersal fish, its foraging shift to pelagic prey results in coupling between pelagic and benthic trophic energy flows.

An increasing number of studies have focused on pelagic–benthic couplings as a central issue in aquatic ecology to understand the mechanisms controlling nutrient cycling and community dynamics in the coastal ecosystems (Hobson et al. 1995; Morata et al. 2008; Gillies et al. 2012). Pelagic resources, such as phytoplankton-derived organic matter, make a significant contribution to zoobenthic production below the euphotic zone through sinking of particulate organic matter and/or vertical feeding migration of demersal nekton (Tamelander et al. 2006). Among aquatic consumers, fish predators play a key role in determining the strength and stability of pelagic–benthic couplings in coastal ecosystems because they can flexibly alternate prey from these two different trophic pathways (Vander Zanden and Vadeboncoeur 2002; Briones et al. 2012).

Polis and Strong (1996) proposed the idea that omnivorous predators can respond to resource subsidies by switching prey between habitats, depending on the relative abundance of allochthonous to autochthonous resources. However, it is important to note that the predators' response to basal resource subsidies is less detectable than that of consumers at lower trophic levels because subsidy effects are attenuated through trophic cascades with increasing trophic levels (Marczak et al. 2007). Contrary to such a general prediction, there are some exceptional cases in which fish predators alternate between autochthonous and allochthonous trophic energy flows in response to the allochthonous input of basal resources (e.g., Nakano et al. 1999; Hamaoka et al. 2010a). Our study demonstrates that the bottom intrusion-induced allochthonous nutrient input can enhance pelagic productivity and subsequently pelagic–benthic coupling by the predator fish *A. japonicum* in the coastal ecosystem through the bottom-up trophic cascading effect.

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