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Long-term changes in the role of threespine stickleback (*Gasterosteus aculeatus*) in the White Sea: predatory fish consumption reflects fluctuating stickleback abundance during the last century

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ABSTRACT

Hypothesis: In the White Sea, predatory fish species have consumed higher proportions of stickleback during historical periods and seasons of high stickleback abundance.

Organisms: Adults, juveniles, and eggs of threespine stickleback (*Gasterosteus aculeatus*), together with three species of predatory fishes: cod (*Gadus morhua*), saffron cod (*Eleginus nawaga*), and European sculpin (*Myoxocephalus scorpius*).

Place and times: Kandalaksha Bay, White Sea, Russia; June to August 2011–2014.

Analytical methods: Sampling with beach seine (stickleback) and gill nets (predatory fish). Analysis of predatory fish stomach contents (identification to the species level, counting, weighing), and in-depth survey of scientific literature on predatory fish diets over the last century.

Results: Near the spawning grounds, stickleback comprise 60% of the summer food of sculpin (adult stickleback), 52% of the diet of cod (adults, juveniles, and eggs), and 15% of the diet of saffron cod (juvenile stickleback). These data resemble observations made during a period of high stickleback abundance in the White Sea (1930–1950s). During a period of low abundance (1960s to early 2000s), stickleback were absent from the stomachs of predatory fish.

Keywords: Atlantic cod, *Eleginus nawaga*, European sculpin, *Gadus morhua*, *Gasterosteus aculeatus*, long-term changes, *Myoxocephalus scorpius*, predation, saffron cod, threespine stickleback, White Sea.

INTRODUCTION

It has been shown that marked changes in the abundance of forage organisms can cause a change in the diets of their predators. For instance, increased abundance of Atlantic herring (*Clupea harengus*) saw their contribution to the diet of cod (Casas, 1996) and pollack (Carruthers

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et al., 2005) increase. Decline in the cladocera *Bosmina longispina* in the Baltic Sea's Gulf of Riga in 2003–2004 and 2006 led stickleback, sprat (*Sprattus sprattus*), and smelt (*Osmerus eperlanus*) to consume more of the copepods *Eurytemora affinis* and *Acartia* spp. In 2005, however, when the abundance of *B. longispina* was high, they appeared in fish stomachs in large quantities (Lankov *et al.*, 2010). Diet composition affects species' overall health. For example, changes in the abundance of different zooplankton species in the northern Baltic Sea affected the growth rate and fat content of herring during the 1980s and 1990s (Peltonen *et al.*, 2004).

Interactions between predator and prey are not limited to their influence on mutual abundance. According to optimal foraging theory, an efficient predator will maximize energetic intake per unit time in line with variation in prey density over time; the theory predicts that the predator will be more selective when prey abundance or density is higher (Emlen, 1966; MacArthur and Pianka, 1966), which results in density-dependent selection. Such selection has been demonstrated empirically (Werner and Hall, 1974; O'Brien *et al.*, 1976; Bartell, 1982; Cunningham *et al.*, 2013). Therefore, changes in prey density may influence patterns of predator selectivity and as a consequence change the phenotypic and genotypic structure of a prey population.

The threespine stickleback (*Gasterosteus aculeatus*) can be an important forage species for predatory fish such as cod [*Gadus morhua* (Almqvist *et al.*, 2010)] and Atlantic salmon [*Salmo salar* (Hansson *et al.*, 2001)]. The growth of stickleback populations may cause an increase or a decrease in the abundance of predatory fish (Nilsson *et al.*, 2004; Ljunggren *et al.*, 2010; Byström *et al.*, 2015), and also induce trophic cascades in shallow lagoons (Jakobsen *et al.*, 2004) and coastal benthic communities (Sieben *et al.*, 2011).

Currently, threespine stickleback are the most abundant fish in the White Sea (Ivanova *et al.*, 2016). This was not the case during most of the twentieth century, however. Studies have shown that stickleback have experienced large-scale fluctuations in abundance. They were very abundant from 1920 to 1960, but declined dramatically in the next decade and sustained very low numbers until the 1990s. At that time, the population expanded again, and is now close to its historical maximum (Lajus *et al.*, 2013).

In the White Sea, stickleback spend most of their lives offshore feeding on plankton, and only come inshore to spawn during the few warm summer months. During this time, adults approach high densities and are actively consumed by predatory fish such as Atlantic cod [*Gadus morhua* (Yershov, 2010a)] and European sculpin [*Myoxocephalus scorpius* (Yershov, 2010b)]. Therefore, spawning stickleback may play an important role in coastal ecosystems via the transfer of nutrients brought in from the open sea. During the first months of their lives, juvenile stickleback form dense aggregations in the coastal zone, and likely are an important source of food for other organisms. However, little research has addressed the role of juvenile stickleback in the food web (but see Demchuk *et al.*, 2015).

Comparing the diet of predatory fish during different historical periods showed that cod and sculpin consumed more adult stickleback when stickleback were highly abundant (Yershov, 2010a, 2010b). Although information is absent on the seasonality of stickleback consumption, strong seasonal abundance suggests that seasonal dynamics should be pronounced. Estimating the importance of stickleback to predators compared with other food items is important for predicting changes in the marine ecosystem due to the proliferation of this species. However, gaps in our knowledge make this task difficult. Although stickleback abundance has changed markedly over the last decades, most recent studies are based on samples collected in 2007–2008, and were not followed up with quantitative population assessments (Lajus *et al.*, 2013). In particular, at Seldyanaya Inlet in Kandalaksha Bay, where we performed our research, the abundance of stickleback increased during the first decade of the twenty-first century, and now fluctuates with about 5-fold amplitude (T. Ivanova, M. Ivanov and D. Lajus, unpublished data).

Historical methods can be useful for reconstructing the past of marine ecosystems (Holm *et al.*, 2010; Schwerdtner Máñez *et al.*, 2014). The historical dynamics of fish populations is studied mostly using the catch data of commercially fished species. For the White Sea, such studies have been conducted for the seventeenth through nineteenth centuries for Atlantic salmon (Lajus *et al.*, 2007a) and herring (Lajus *et al.*, 2007b). Many non-commercial species, such as stickleback, have an important part to play in ecosystems, but long time-series data are not available for these species [for an exception in the Baltic Sea, see Lajus *et al.* (2015)]. Data on the diet of predatory fish may be an important source of information for such species. White Sea stickleback are an exception because information on their abundance is quite rich (Lajus *et al.*, 2013). However, analysis of stomach contents, associated with survey data on prey abundance, is important for verifying this approach, and is also an independent source of information for the historical reconstruction of spatial and temporal patterns of prey abundance.

Therefore, the goal of this study is to trace the association between threespine stickleback abundance in the White Sea and their contribution to the diets of predatory fish based on literature and original data. We test the hypothesis that the significance of stickleback as prey to predatory fish will increase in periods of high stickleback abundance.

METHODS AND MATERIALS

Study site and field sampling

Sampling was conducted at Seldyanaya Inlet in Kandalaksha Bay in the White Sea (66°20′15″N, 33°37′28″E; Fig. 1). In addition to our own data, we analysed all available literature on the feeding of three species of predatory fish in the White Sea: Atlantic cod (*Gadus morhua*), saffron cod (*Eleginus nawaga*), and European sculpin (*Myoxocephalus scorpius*). Sampling locations and times for previous studies are presented in Fig. 1.

Seldyanaya Inlet is a typical small inlet about 0.5 km long and less than 5 m deep at its outlet to the sea. Dense eelgrass (*Zostera marina*) beds (density ~5 $kg \cdot m^{-2}$) cover approximately half of the inlet; such habitat typically supports a high density of threespine stickleback (Lajus *et al.*, 2013; Ivanova *et al.*, 2016). Population density was measured using a 7.5-m long beach seine with wings 1.5 m high, and a mesh-size of 5 mm on the wings and 1 mm in the cod-end. We sampled an area of 120 m^2, with a catch efficiency of 0.6. Catch efficiency was measured using mark–recapture techniques (Lockwood and Schneider, 2000) in a small lagoon (T. Ivanova, M. Ivanov and D. Lajus, unpublished). Samples were collected weekly in June and July 2009, and in July to August 2007–2014.

Predatory fish were sampled in June to August 2011–2014, using a set of four gill nets with mesh sizes of 16, 20, 30, and 40 mm respectively, each 30 m long and 1.5 m high. Nets were set from the shore at a depth of 5 m. The duration of exposure was about 12 hours (usually from 21.00 to 09.00 hours). In total, our sample consisted of 111 cod, 59 saffron cod, and 54 sculpin. The size structure of these fish is presented in Fig. 2. Most were aged 3+ and 4+ years, with only a few individuals aged 2+ and 5+ years.

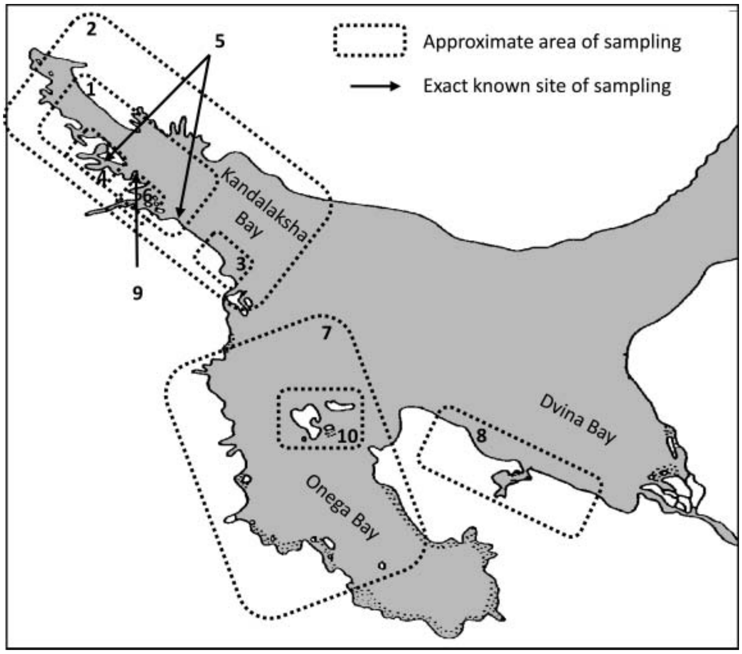

Fig. 1. Locations and study periods of fish feeding on stickleback. **Cod:** sample area 1: 1932–33 (Yevropeitseva, 1937); 2, 10: 1951 (Sonina, 1957); 3: 1950s (Kudersky, 1966); 4: 1960s (Izvekova, 1964); 5: 1986 (Parukhina, 2005); 6: 2007 (Yershov, 2010a); 9: 2011–14 (our data). **Saffron cod:** 7, 8: 1941–43 (Palenichko, 1949); 7: 1951–52 (Timakova, 1957); 7: 1961–62 (Kudersky and Anukhina, 1963); 9: 2011–14 (our data). **Sculpin:** 4: 1948–55 (Kudersky and Rusanova, 1963); 4: 1960 (Rogacheva, 1961); 4: 1989–91 (Poltermann, 1992); 6: 1998 and 2007–8 (Yershov, 2010b); 9: 2011–14 (our data).

Sample processing

Body mass was recorded to within 0.1 g and total body length measured to within 0.1 cm. Fish age was calculated from otoliths to allow determination of dominant age groups. Stomachs were removed and fixed in 4% formaldehyde. Prey organisms were identified to the lowest possible taxon, then counted and weighed. We measured the role of particular prey items in the diets of fish using frequency of occurrence (F_i) and relative wet mass (I_i) (Hyslop, 1980). Frequency of occurrence was estimated according to the formula:

$$F_i = 100N_iN^{-1},$$

where N_i is the number of fish with the food category i in their stomachs, and N is the total number of fish found. Relative wet mass was calculated as follows:

$$I_i = 100S_iS_t^{-1},$$

where S_i is the mass of food category i, and S_t is the total mass of the stomach contents. Feeding patterns were visualized using Costello plots (Costello, 1990).

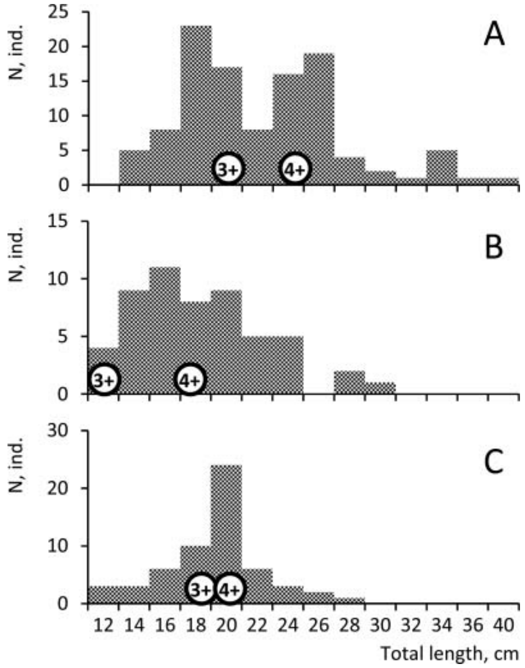

Fig. 2. Size distribution of predatory fish sampled for diet analysis: (A) Atlantic cod *Gadus morhua*, (B) European sculpin *Myoxocephalus scorpius*, (C) saffron cod *Eleginus nawaga*. Circles indicate fish age, and their position denotes the average length of fish at this age.

Determining the seasonal (summer) role of stickleback in the diets of predatory fish

The role of stickleback in the diets of predatory fish was estimated for 3-year-old specimens, the most numerous age group for each sampled species. For each month of the year, we calculated the nutritional needs of predators using the balance equation (Borutsky, 1974; Vinberg, 1984):

$$C = P + R + F,$$

where C is consumption, P is production (increase in body mass), R is the cost of metabolism, and F is the undigested portion of food.

All items were calculated in grams per month. Production was derived from increased body mass, taking into account that growth continues from May to October. Cost of metabolism was based on current body mass and average water temperature during each month, obtained from the website www.rp5.ru. The undigested portion of food was assumed to be 20% of the diet – the average for predatory fish according to Vinberg (1956). From these figures, we derived the dietary requirements of one individual predatory fish in a particular month. Finally, we determined the total weight of stickleback consumed during the study period (June to August) based on the proportion of stickleback in the stomach contents of predatory fish each month.

RESULTS

Seasonal dynamics of stickleback

In late May or early June, threespine stickleback appear in great numbers in the coastal zone of the White Sea, especially in Kandalaksha Bay (Ivanova *et al.*, 2016). Spawning occurs from mid-June to mid-July. Most spawners are 2–3 years old, with some reaching 4 years of age. About 20% of the spawning fish are 1 year old, but not all fish of this age take part in spawning. For the most part, 1-year-old fish (83%) do not appear on the spawning grounds (for more details, see Ivanova *et al.*, 2016). After spawning, adult fish leave the inshore zone – first females and then males, which guard the nests and hatched larvae that appear in early to mid-July. By early August, juveniles are 10–15 mm long and weigh 20–40 mg. Dense shoals of juvenile stickleback feeding in shallow inlets, often associated with eelgrass beds, are observed during the first 3 weeks of August (Rybkina *et al.*, submitted). In mid-August, having attained a length of 20–25 mm and mass of 80–100 mg, juvenile stickleback start their offshore migration, and have abandoned the inshore entirely by the second half of September (Fig. 3).

We collected samples of predatory fish during the different periods of inshore stickleback presence: (1) high spawner density in the second half of June; (2) low spawner density in July, with small juveniles present; (3) high densities of mature juveniles in first half of August; and (4) marked reduction in juvenile density due to their offshore migration in late August.

Fish communities in the coastal zone

During 4 years of field sampling and fish stomach contents analysis in the coastal zone of Seldyanaya Inlet, we detected 15 species of predatory fish (Fig. 4), eight of which consumed stickleback. For species to be selected for further study, they had to meet two criteria: (1) threespine stickleback were to be an important component of their diet, and (2) they had to be abundant enough to provide representative quantitative data for the analysis of the dietary role stickleback play in that species. Based on these criteria, we selected the following species for further analysis: Atlantic cod, saffron cod, and European sculpin. Low-abundance fish also preyed on stickleback, such as Asiatic smelt (*Osmerus dentex*), Arctic staghorn sculpin (*Gymnocanthus tricuspis*), European whitefish (*Coregonus lavaretus*), and brown trout (*Salmo trutta*). Occasionally, stickleback appeared in the stomachs of two relatively abundant species: fourhorn sculpin (*Triglopsis quadricornis*: adult stickleback) and Pacific herring (*Clupea pallasii*: juvenile stickleback). No stickleback were observed in the stomach contents of other fish species, with one exception. We often observed cases of cannibalism, where adult stickleback preyed on their own eggs, but we do not consider this here.

Feeding patterns of predatory fish

Atlantic cod

During the stickleback spawning season, cod actively consumed adult stickleback and their eggs (Fig. 5A). High consumption ratios of eggs (50%) to adult stickleback (20%), and the shape of egg globes in cod stomachs showed that these predators not only consumed gravid

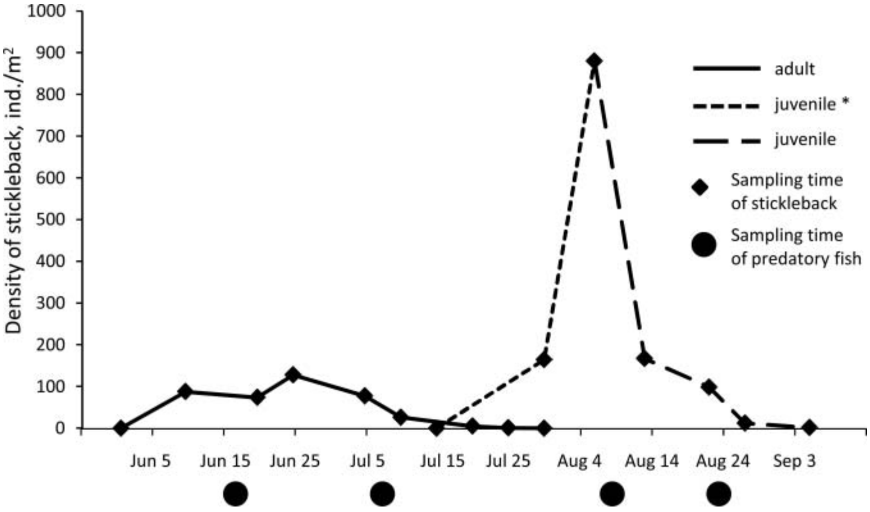

Fig. 3. Seasonal dynamics of stickleback on spawning grounds, with sampling times for stickleback and predatory fish (in different years, sampling timing could shift 2–3 days). *Density of juveniles was underestimated because small fish (less then 12 mm) passed through the mesh of beach seines deployed for sampling.

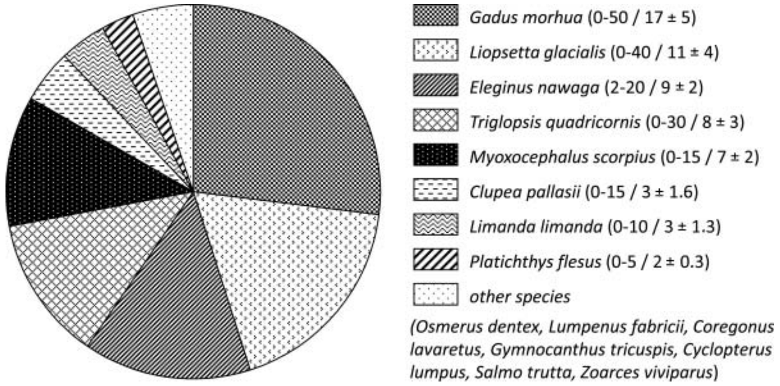

Fig. 4. Predatory fish species sampled in the Keret Archipelago coastal zone of the White Sea, June/August 2011–14. Figures in parentheses represent the number of fish per one set of gill nets (range / mean ± standard error) (see text for explanation).

females, but also took eggs from nests. At this time, mostly adult stickleback were found in cod stomachs. In the second half of the summer, cod switched to abundant juvenile stickleback. In late August, as juveniles left the inshore zone, adult stickleback reappeared in the diet of cod – likely fish that had lingered close to the spawning grounds. Other fish, primarily slender eelblenny (*Lumpenus fabricii*), also appeared in the diet of cod at this time. The proportion of cod with empty stomachs during summer did not exceed 15%.

Analysis of Costello plots presenting both frequency of occurrence of food items (F_i) and their relative wet mass (I_i) shows that cod do not have clear core food items: all significant taxa (fish, polychaetes, and crustaceans) occur relatively evenly in their diet during the

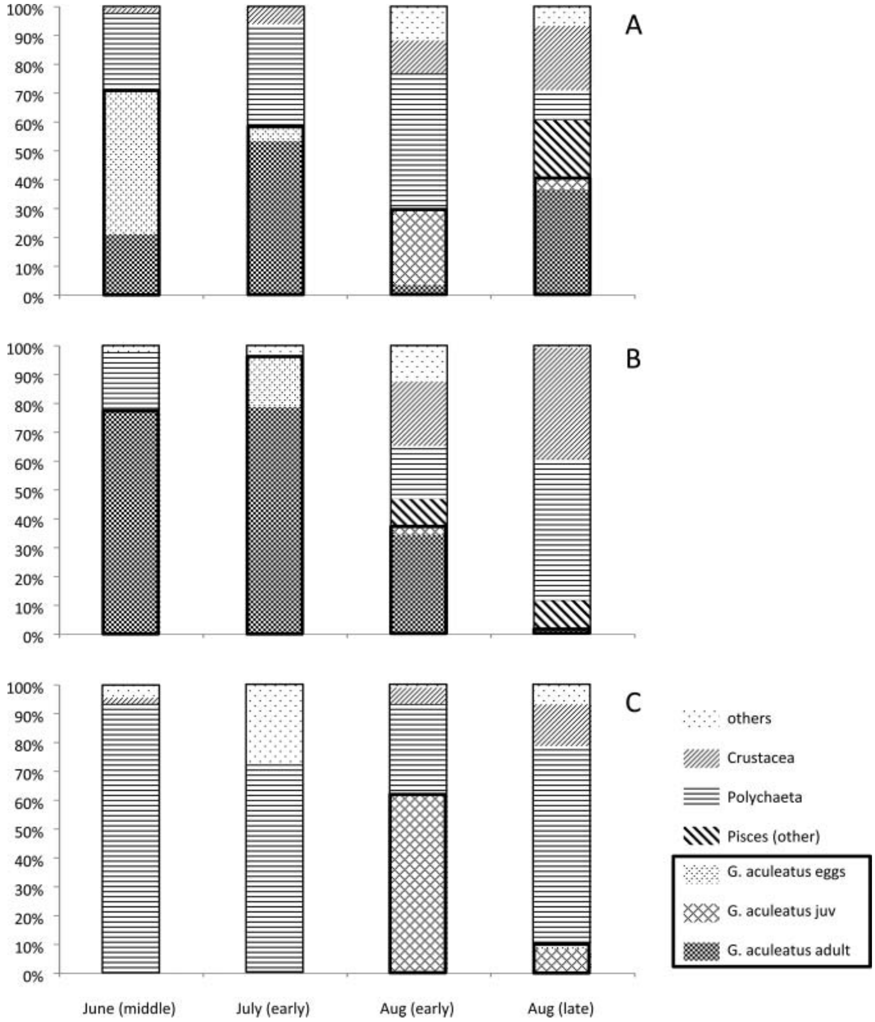

Fig. 5. Proportions of different prey organisms in the stomach contents (percentage of wet mass) of three predatory fish species: (A) Atlantic cod, (B) European sculpin, (C) saffron cod.

summer season – that is, cod easily switch between prey, and their diet is rather diverse at all times (Fig. 6A).

European sculpin

Adult stickleback comprised the main part of sculpin diets during the period of high stickleback abundance in the coastal zone from early June until mid-July (Fig. 5B): adults occurred in all sculpin stomachs (Fig. 6B). However, unlike cod, sculpin took many fewer stickleback nests. In June, eggs in sculpin stomachs were uncommon, and in July egg mass did not exceed 20% of the mass of all forms of stickleback in sculpin stomachs. Even more important, sculpin did not prey on abundant juvenile stickleback after adults had left the inshore zone. They switched to polychaetes and crustaceans, and specimens with empty stomachs increased from 0% in June/July to 53% in August (*t*-test, $P < 0.005$).

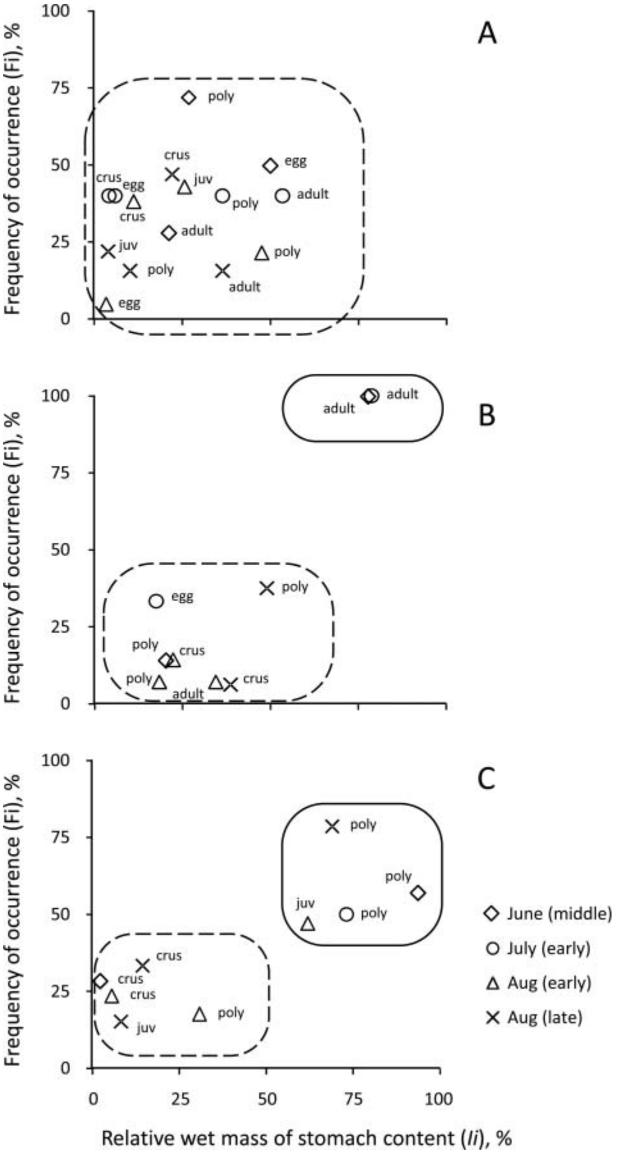

Fig. 6. Feeding characteristics of three species of predatory fish in the White Sea at different times in the summer season (Costello plots): (A) Atlantic cod, (B) European sculpin, (C) saffron cod. Food items: adult = adult threespine stickleback; juv = juvenile threespine stickleback; egg = eggs of threespine stickleback; poly = Polychaeta; crus = Crustacea. Solid lines delineate core food items (frequent occurrence and a high proportion of stomach content mass); dashed lines delineate minor food components.

Saffron cod

During summer, this species fed mostly on polychaetes, in particular *Nereis pelagica* and *Alitta virens*, which comprised more than 60% of Polychaeta wet mass. Polychaetes predominated by weight and occurrence, forming the core of saffron cod food items

Table 1. Summer diets of three predatory fish species in the Keret Archipelago, White Sea

Species	Mass (g)	*P* (g per year)	*R* (g per year)	*C* (g per year)	*C* (g in summer season)	Stickleback as percentage of diet			
						Adult	Juvenile	Eggs	Total
Cod	104	91	341	541	243	5.8	15.8	52.8	5.8
Sculpin	36	72	185	322	142	0.5	5.2	61.3	0.5
Saffron cod	56	9	172	227	102	14.4	0.3	14.8	14.4

Note: All calculations were performed for 3-year-old specimens. *P* is production (increase in body mass), *R* is the cost of metabolism, *C* is consumption.
See evolutionary-ecology.com/data/2991Appendix.pdf

(Fig. 5C and 6C). Only during a short period from early to late August did the very abundant juvenile stickleback replace polychaetes to become the main component of the saffron cod diet. Saffron cod rarely preyed on adult stickleback. In addition to polychaetes and stickleback, saffron cod fed on crustaceans, which occurred in 20–30% of stomachs, but comprised only a minor part in terms of mass. Saffron cod fed evenly during summer and, like cod, the number of non-feeding individuals did not exceed 15%.

The role of stickleback in the diet of predatory fish

To assess the significance of stickleback in the feeding regimens of these predatory fish, we analysed their diet in summer (June to August), including the proportions by mass of stickleback adults, juveniles, and eggs (Table 1). Stickleback made up 60% of the diet of sculpin in summer. In cod, this fell to 52%, consisting mostly of adult fish, although juveniles and eggs were also important. In saffron cod, stickleback comprised just 15% of their summer diet, made up almost entirely of juveniles. Note that data for the other seasons of the year are not available.

DISCUSSION

The role of stickleback in the diets of predatory fish in the White Sea, 1930s to the present day

Detailed critical analysis of published materials on stickleback consumption by predatory fish in the White Sea during periods of high and low stickleback abundance is provided online (evolutionary-ecology.com/data/2991Appendix.pdf). These publications are not numerous and not all data in them are comparable. All available data on predatory fish feeding on threespine stickleback in the White Sea is summarized in Fig. 7. Using these data, we analysed fish feeding patterns to determine the role of stickleback abundance in the diets of their White Sea predators. To facilitate comparisons of long-term time series, we selected the most representative summer month of each predator. For cod and sculpin this is June (Fig. 5), when these species actively feed on adult fish and eggs on the stickleback spawning grounds. For saffron cod, we selected August because this species feeds on juvenile stickleback, which are abundant on the spawning grounds at this time.

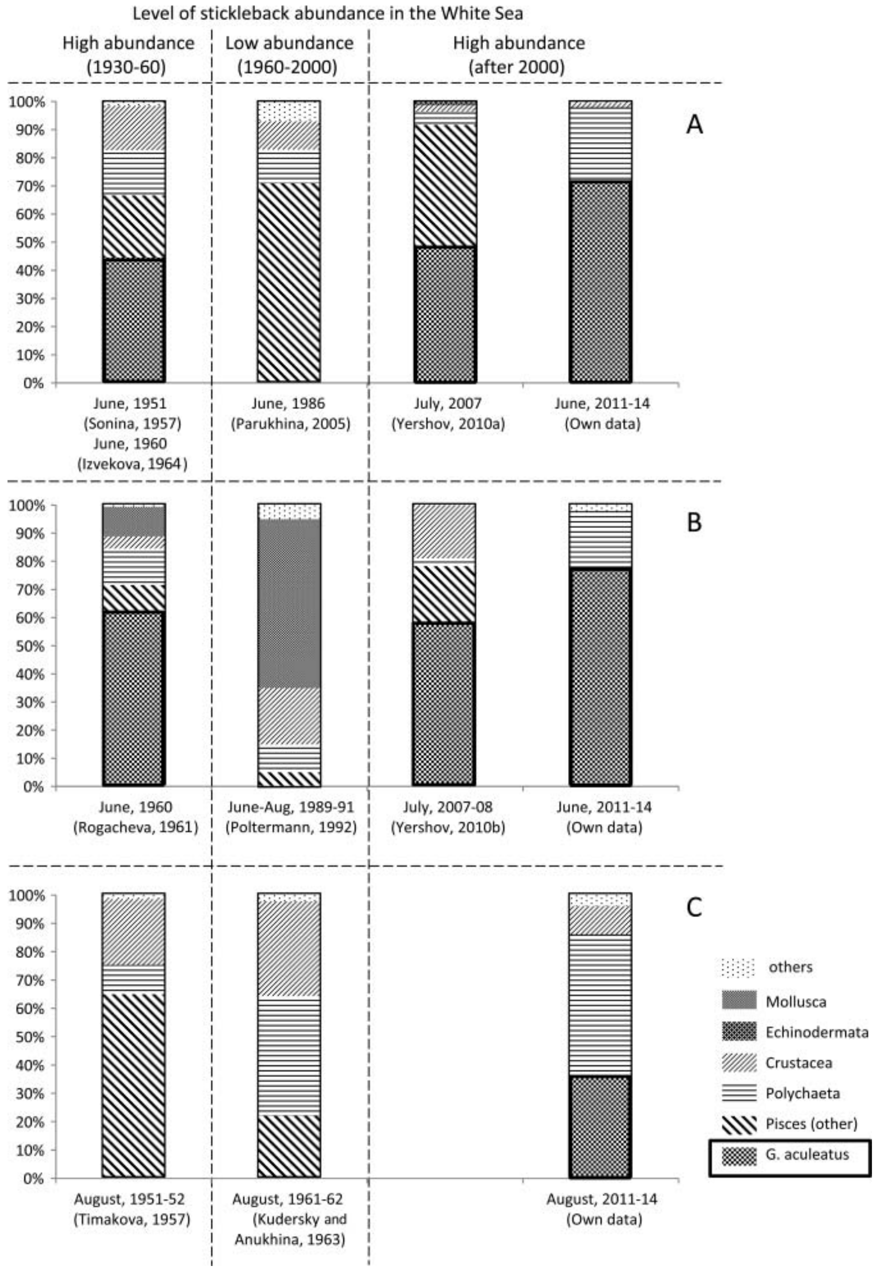

Fig. 7. Stomach contents of predatory fish in the White Sea, during years of different stickleback abundance (based on published data and our new surveys): (A) Atlantic cod, (B) European sculpin, (C) saffron cod.

Atlantic cod

During periods of high abundance, stickleback formed an important component of the diet of cod, comprising 35–50% of their stomach contents. Fish make up a high proportion of the cod diet in general, and stickleback represent more than half of it. Notably, up to 50% of the cod diet is comprised of stickleback eggs in June (Fig. 5A). Since such a high proportion cannot be explained by the eggs of gravid female stickleback alone, for which the gonadosomatic index during the spawning period is about 25% (Yershov, 2011), cod must intentionally prey on stickleback nests. In the absence of stickleback, cod replaced them with other fish such as herring, saffron cod, sculpins, butterfish, and slender eelblenny. The contribution of invertebrates to the cod diet did not change with stickleback abundance. It has been reported that cod change food preferences in line with fluctuations in the availability of prey: they simply shift to more abundant food items (Hanson and Chouinard, 2002). Our results confirm this (Fig. 6A). Modern data are similar to data from the 1940s and 1950s (Fig. 7A), but our data and those of Yershov (2010a) do differ. According to Yershov, the percentage of fish overall in the cod diet is higher than in our samples, although the proportion of stickleback in our samples is higher. The differences between the studies could arise because Yershov (2010a) caught cod at a greater depth (from 5 to 25 m), whereas our samples were collected at a depth of 5 m where stickleback are more abundant, or because the average size of cod in our samples is 22 cm, less than the 32 cm average of Yershov's samples.

European sculpin

In periods of high abundance, stickleback represented from 40 to 70% of the diet of sculpin. When stickleback declined, sculpin, unlike cod, did not replace stickleback with other fish species, instead markedly increasing the proportion of benthic organisms (molluscs and crustaceans) in their diet. According to our data, in June and early July stickleback comprised close to 100% of the sculpin diet (Fig. 5B). It would seem that stickleback represent an ideal food source for a small ambush predator inhabiting shallow water in the coastal zone. Moreover, sculpin, unlike cod, rarely consume stickleback eggs. The small amount of eggs found in sculpin stomachs can be explained by their consumption of gravid stickleback females. Sculpin specialize in motile prey rather than stationary objects. When stickleback are absent, sculpin switch to the benthos for food, and this may result in decreased growth and abundance (Poltermann, 1992). We have no direct evidence to support this assumption, although a similar situation occurs during seasonal stickleback migration offshore. Rather than switch to other prey like cod, sculpin decrease feeding activity (we observe more empty stomachs). Interestingly, in August, stickleback are present in some cod stomachs, but not in those of sculpin. This could mean that stickleback are distributed in deeper waters close to shore, where they are unavailable to shallow bottom predators such as sculpin.

Saffron cod

In general, saffron cod do not rely to a great extent on stickleback, despite consuming a significant amount of them during a few weeks in late summer, when threespine stickleback juveniles comprise up to 30–40% of their diet (Fig. 7C). Timakova (1957) reported that during August of 1951 and 1952, juvenile stickleback were very abundant (often exceeding 50%) in the stomachs of saffron cod, but the author presented only pooled data for all fish.

Based on our data, we assume that at least half of the August diet of saffron cod consists of threespine stickleback. Although there is little information on the feeding of saffron cod in the White Sea, we suggest that changes in stickleback abundance do not influence the saffron cod population. This fish feeds mostly on polychaetes, and dietary habits change little after stickleback juveniles migrate offshore in August.

Threespine stickleback play a different role in the diets of Atlantic cod, European sculpin, and saffron cod. Atlantic cod are large mobile predators that actively search for prey, switching very easily from one prey to another depending on their abundance. They prey on adult stickleback and eggs during spawning, and later on juveniles. These are the hallmarks of an opportunistic predator (Scott and Scott, 1988), and our research confirms this. As an ambush predator, sculpin feed only on adult stickleback and depend on them more than on other species, both in terms of the percentage of stickleback in their diet and the ability of sculpin to switch to other prey. Sculpin do not feed on juvenile stickleback, likely because targeting tiny juvenile stickleback results in little energetic gain. It seems that sculpin abundance depends to a great extent on stickleback. In contrast, saffron cod specialize in feeding on benthic organisms and eat juvenile stickleback, but adult stickleback may be too large and too well protected for this species. These very different feeding strategies suggest that stickleback abundance may play a role in shaping the predatory fish community in the White Sea.

We could potentially underestimate the role of juveniles as prey because of their rapid passage through the stomachs of predatory fish, which may spend up to 12 hours in a gill net after capture. We estimated the duration of gastric digestion based on formulae provided by Tseitlin (1980). For calculations we used the most probable parameters from our field observations. Saffron cod provide an example: number of juveniles in stomach = 3, mass of one juvenile = 40 mg, mass of predator = 100 g, water temperature = 14°C. We estimated the time of gastric digestion to be 10 hours. As this is less than the time spent in gill nets, juvenile consumption may be underestimated, but probably not by more than a few percentage points. Identifying stickleback in stomachs may be possible over longer periods of time due to well-preserved dorsal spines, which are recognizable long after soft tissue has been digested.

About half of the stickleback population do not take part in spawning – these are immature fish (Ivanova *et al.*, 2016) that spend their first year offshore. In the White Sea, there is no abundant pelagic fish predator to feed on this portion of the stickleback population. We believe that their role is to compete with other pelagic species – principally Atlantic herring – and to accumulate nutrients and energy to take to the coastal zone as adults.

Finally, the role of stickleback in the diet of predatory fish depends not only on their abundance, but also on availability. This depends on the year-to-year timing of their spawning migration, and on their distribution over suitable habitat. Changes in timing and geographic distribution may affect the stickleback's susceptibility to predation. Our field observations confirm fluctuations in the start of the spawning migration of stickleback, but by a non-significant amount [up to one week (T. Ivanova, M. Ivanov and D. Lajus, unpublished data)]. Although these factors add noise (a significant consideration in short time series), they are less important in long-term comparisons given the magnitude of fluctuations in abundance (Haidvogl *et al.*, 2014).

CONCLUSION

We observed a high correlation between the abundance of stickleback and their presence in the stomachs of predatory fish. Patterns of correlation are similar when comparing seasonal dynamics with long-term changes. The responses of predatory species are basically the same whether stickleback disappear due to shifts in seasonal dynamics or long-term changes in abundance. For cod, stickleback comprise about half of their summer diet in periods of high abundance, but when stickleback are not available cod simply switch to other fish prey. Stickleback occupy an even more important place in the diet of sculpin. This species cannot adequately replace stickleback with other prey, and markedly decreases its feeding activity in the absence of adult stickleback. For saffron cod, juvenile stickleback represent an additional food source when they are especially abundant. Several other White Sea fish species feed on stickleback, but they are either not particularly abundant themselves or consume stickleback only occasionally. Among birds, stickleback are important food items for Arctic terns (*Sterna paradisaea*) and herring gulls (*Larus argentatus*), which prey on other fish as well (G. Tertitsky, personal communication).

What are the consequences of the marked increase in the stickleback population observed in recent decades in the White Sea ecosystem? It is likely that there will be an increase in stickleback predators. These include European sculpin, for which stickleback are an important prey item, and which spend much of their time in the shallow coastal zone during warm periods. However, growth in the population of the small omnivorous stickleback should also result in increased zooplankton consumption, greater competition with other pelagic fish such as herring (Peltonen *et al.*, 2004; Lefébure *et al.*, 2014), predation on the eggs and larvae of other fishes (Kotterba *et al.*, 2014; Byström *et al.*, 2015), and increased growth of filamentous algae in coastal zones that may suppress seagrass and kelp (Ritchie and Johnson, 2009; Baden *et al.*, 2012). Many different processes are engaged in ecosystem responses to the changing abundance of a prolific species. In this instance, some responses might limit available food, or transmit parasites from stickleback to their predators, including the cestode *Bothriocephalus scorpii* and nematodes (Shulman and Shulman-Albova, 1953; Rybkina *et al.*, 2016).

An association between the spatial abundance of prey fish and their presence in the stomachs of predators can be used in research to analyse the distribution of prey, as was demonstrated for cod and capelin (Fahrig *et al.*, 1993). The influence of predators on prey species is also key, not only in terms of changing abundance, but also life histories (Heins *et al.*, 2016). Moreover, predators may change the phenotypic and genotypic structure of stickleback populations through their choice of prey being dependent on stickleback abundance, which is a consequence of optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966). White Sea stickleback and their predators represent a rare case when such associations can be studied using historical time series. Our study demonstrates this association qualitatively, but further field studies on the feeding patterns of predatory fish and the abundance of stickleback will allow us to address this question quantitatively, and to effectively use these data to analyse temporal change.

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