Chapter 2
Feeding and Digestion

Abstract Obtaining food for energy is essential for all living things that don't photosynthesize. Reduced feeding and digestion are commonly observed after exposure to a variety of pollutants. Alterations in feeding, nutrient assimilation, and energetics in many species could not only impact their own population dynamics, but also could have community-wide repercussions. Decreased feeding is not only a general response to contaminants, but also can result in a "positive feedback" situation, since poor nutrition resulting from decreased feeding can in turn make animals more susceptible to contaminants (Dissanayake et al. Aquat Toxicol 89:40–46, 2008). These authors advised that "ecotoxicological studies need to take into account the nutritional state of the test organism to achieve the full assessment of contaminant impact." On the other hand, it is also likely that decreased feeding will reduce further uptake of contaminants. This is particularly true for animals at higher trophic levels, which acquire much of their body burden of contaminants from their food. Additional discussion of pollution effects on feeding is covered in Chap. 9, Behavior.

Keywords Assimilation • Consumption • Enzymes • Feces • Filtration • Foraging • Growth • Gut fluid • Intestinal transport

2.1 Feeding

2.1.1 Crustaceans

Reduced food consumption is an almost universal response in crustaceans to many toxicants (Taylor et al. 1993; Maltby and Crane 1994; Wallace et al. 2000). However, increased feeding rates have occasionally been observed, e.g., in amphipods exposed to the chlorinated pesticide lindane (Blockwell et al. 1998).

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Metals

Chronic exposure to copper ($>85\ \mu g\ l^{-1}$) and zinc ($>106\ \mu g\ l^{-1}$) reduced growth of shrimp larvae (*Farfantepenaeus paulensis*) because of reduced feeding (Santos et al. 2000). Both metals reduced the number of *Artemia* captured by the shrimp larvae during 30 min. Oxygen consumption also was reduced by about 30 % in all concentrations. Similarly, gut fullness of shrimp, *Metapenaeus ensis,* larvae feeding on the diatom *gracilis* was reduced by a 2-h exposure to copper at 0.25 mg l^{-1} (Wong et al. 1993).

In contrast, gut fullness of larvae was not affected even after 24-h exposure to chromium or nickel at high concentrations close to the 48-h LC_{50} (5.41 and 1.28 mg l^{-1}, respectively). However, postlarval shrimp exposed for 24-h to those concentrations of Cr, Cu or Ni consumed fewer *Artemia* nauplii. While younger stages are generally more sensitive than older stages, this obviously depends on the species and toxicant. Blue crabs, *Callinectes sapidus*, were fed grass shrimp *Palaemonetes pugio* contaminated with 1.8 μg TBT, 0.09 μg DBT (dibutyltin) and 0.03 μg MBT (monobutyltin) g^{-1} wet weight tissue. Feeding rates for exposed and control crabs were equal during the 16-day test (Rice et al. 1989). Growth, molting success and feeding rates were not affected. Catabolism of TBT reduced tissue concentrations of TBT, thereby increasing the tolerance of blue crabs to TBT.

Organics

Jensen and Carroll (2010) examined feeding of copepods exposed to the water-soluble fraction (WSF) of crude oil. Feeding was inhibited in *Calanus finmarchicus* exposed to 0.4 μg l^{-1} of the WSF, showing that adults are sensitive to exposure to crude oil well below saturation level. Effects of PCBs on estuarine shrimps were investigated by Nimmo et al. (1975). Toxicity tests showed estuarine species to be sensitive at low concentrations in water, with shrimps (*Penaeus duorarum, P. aztecus*, and *Palaemonetes pugio*) affected at or near 1 μg l^{-1}. Exposed shrimp later became lethargic and stopped feeding. It is possible that the lethargy was due to non-polar narcosis, which could have caused the reduced feeding. It is also possible that the reduced activity (lethargy) was due to low energy levels from reduced feeding.

Hypoxia

Feeding by the mud crab *Neopanope sayi* and juvenile blue crabs *Callinectes sapidus*, decreased during hypoxia, suggesting that short hypoxic episodes may create predation refuges for their prey (Sagasti et al. 2001). This was supported by mesocosm studies by Seitz et al. (2003) using blue crabs and *Macoma balthica* clams. Predation on clams was significantly lower under low DO (<2 mg $O_2\ l^{-1}$)

than under normoxia. Thus, under short-term hypoxia, both crab feeding efficiency and trophic transfer from *M. balthica* to blue crabs were reduced. Changes in clam burial depth due to oxygen levels were determined by establishing normoxic and low DO levels in replicate aquaria. Burial depth after 48 h exposure did not differ as a function of oxygen level. None of the clams died after 2 days in low DO, 27 % died after 6 days, and 90 % died after 21 days. Authors concluded that short-term hypoxia therefore reduces the ability of crabs to forage upon clams efficiently and increases clam survival, whereas long-term hypoxia may increase the availability of clams to predators through mortality and movement to the surface. Bell et al. (2003) used biotelemetry and measurements of dissolved oxygen to monitor the feeding and movement responses of free-ranging blue crabs *Callinectes sapidus* to episodic hypoxic events and subsequent relaxation events within the Neuse River Estuary, North Carolina, USA. Although crabs did feed in water with DO as low as 1.01 mg l^{-1}, the feeding declined slightly in mild (2–4 mg l^{-1}) and severe hypoxia (<2 mg l^{-1}). Crabs reduced the proportion of time spent feeding during hypoxic conditions. However, the proportion of time crabs spent feeding did not increase and crabs did not reinvade deeper water habitats when DO increased, as had been hypothesized. No significant difference occurred in the feeding rates of blue crabs exposed to normoxia, 119 and 73 Torr O_2, but these rates were significantly higher than that of blue crabs exposed to 50 Torr O_2. [Unfortunately, different investigators use different measurements for DO. Torr is a measurement of pressure, defined as $^1/_{760}$ of one atmosphere; a pressure of 1 Torr is approximately equal to one mm of mercury. In this book the units utilized by the investigator will be used.] Feeding rates in the lesser blue crab (*C. similis*) exposed to 50 and 25 Torr O_2 were significantly lower than in crabs exposed to 119 Torr O_2 and normoxia (Das and Stickle 1993). The feeding rate of crabs after being exposed to hypoxia for 10 days increased sharply upon transfer to normoxic water; however, this may have been due to partial starvation during hypoxia.

Climate Change/Acidification

Effects of 650, 1,250 and 3,500 μatm CO_2 on feeding of shore crabs *Carcinus maenas*, were examined after exposure of both the predators and their prey, the blue mussel *Mytilus edulis*, for 10 weeks. Intermediate levels had no significant effect, but the highest level reduced feeding by 41 % (Appelhans et al. 2012). Active extracellular pH compensation by means of bicarbonate accumulation was observed in the crabs.

In contrast to the effects of hypoxia and acidification on shore crabs, the copepod, *Centropages tenuiremis*, increased both its feeding and respiration rate at elevated CO_2 (1,000 μatm), and associated acidity (pH 7.83), (Fig. 2.1) except for an initial acclimation period, when it fed less (Li and Gao 2012). The authors suggest that copepods increase their respiration and feeding in response to acidification in order to balance the energy costs associated with increased acidity and CO_2.

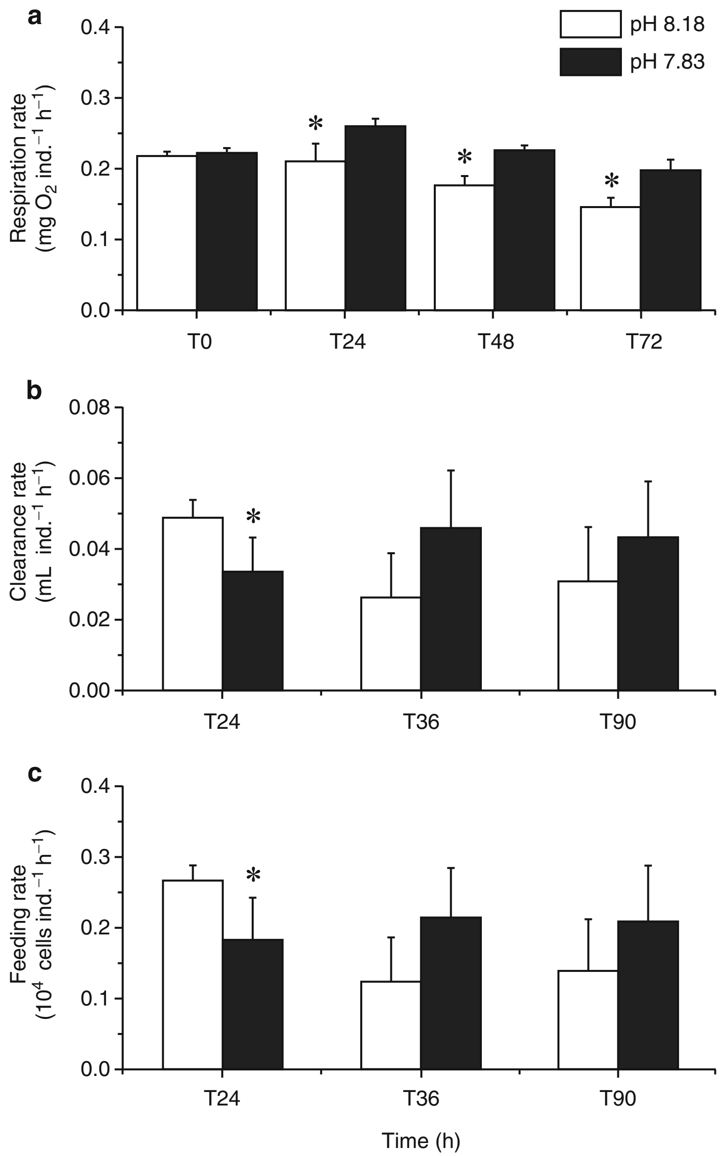

Fig. 2.1 Rates of respiration and feeding by *C. tenuiremis* under ambient (pH 8.18) and acidified (pH 7.83) conditions. (**a**) Respiration, (**b**) clearance, and (**c**) feeding rates of *C. tenuiremis*. *above the columns = significant ($p < 0.05$) differences between the two pH treatments. Vertical bar = SD (From Li and Gao 2012: 702, reprinted courtesy of Elsevier Publishing Co)

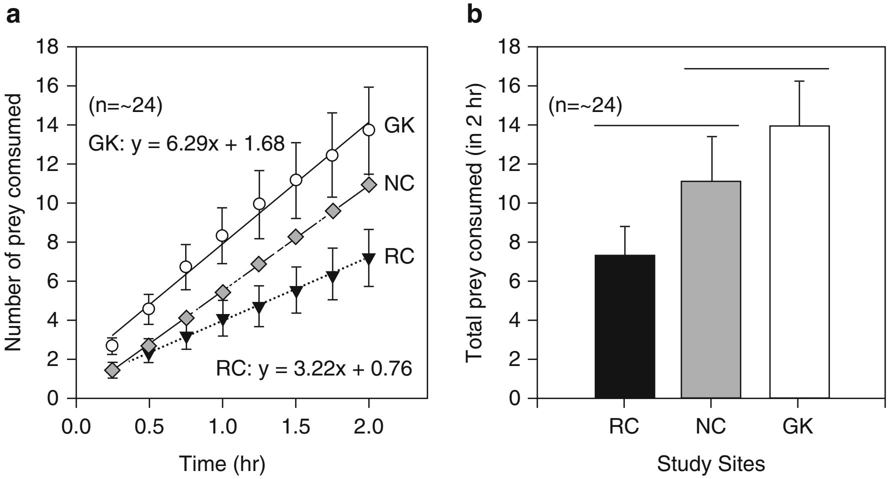

Fig. 2.2 Comparison of (**a**) number of prey (*Artemia francescana*) consumed as a function of time, and (**b**) total prey consumed over a 2-h trial for grass shrimp from Great Kills (GK – *open circle* and *bar*), Nassau Creek (NC – *half tone diamond* and *bar*) and Richmond Creek (RC – *full tone triangle* and *bar*). Mean ± SE. Results of linear regressions for GK and RC in panel A. Lines above bars in B = non-significance ($p > 0.05$) (Reprinted from Perez and Wallace 2004: 84, courtesy Springer Publishing Co)

Impacts in Polluted Sites

A number of studies have assessed feeding rates in animals living in contaminated sites. Perez and Wallace (2004) found that grass shrimp (*Palaemonetes pugio*) from a clean reference site (Great Kills) captured brine shrimp at about twice the rate as grass shrimp from more contaminated sites (Fig. 2.2).

Grass shrimp from the clean site that were maintained in the laboratory for 8 weeks with sediment and water from the contaminated site reduced their feeding to that typical of shrimp from that site, showing that the behavioral difference was caused by the environment. Videotape analysis indicated that reduced feeding was due to shrimp using a less efficient grab type of capture, rather than a lunge or pursuit type of attack. Khoury et al. (2009) compared feeding rate (number of scoops of substrate) of fiddler crabs (*Uca pugnax*) from a contaminated site and a reference site. Crabs from the reference site performed twice as many scoops (on the same sediment) than crabs from the contaminated site. Blue crabs (*Callinectes sapidus*) from a contaminated site captured fewer active prey (killifish or juvenile blue crabs) compared with crabs from a cleaner reference site, but ate comparable amounts of less active prey (fiddler crabs and mussels) (Reichmuth et al. 2009). Gut content analysis showed that blue crabs from the contaminated site ate less fish and crabs but much more detritus, algae, and sediment than crabs from the cleaner site. These food items are not typical for this predatory species. Transplanting "polluted" crabs to the clean site or maintaining them in the laboratory with food from the clean site, caused a reversal in behavior – “polluted” crabs increased their feeding on juvenile blue crabs. Conversely, transplanting reference site crabs to the polluted site or maintaining them in the lab on food from the polluted site caused them to decrease their feeding; this was correlated with bioaccumulation of mercury.

Cellular activity, immune function, cardiac activity, and foraging behavior were studied in green crabs, *Carcinus maenas,* collected from a PAH-contaminated site and two comparatively clean field sites and compared with responses of crabs exposed in the laboratory to the PAH pyrene as a model organic contaminant (200 μg l^{-1}) for 28 days (Dissanayake et al. 2010). Cellular function (hemocyte membrane integrity) and immune function (phagocytosis), were decreased by pyrene exposure in the laboratory. In the field, however, no significant cellular or physiological impacts were seen in the contaminated site, but foraging behavior was significantly reduced, demonstrating that feeding behavior is a more sensitive response (Fig. 2.3). Crabs from the contaminated site (PLYM) took significantly longer than other field-collected and laboratory-exposed crabs to approach a cockle and break the shell, causing longer prey handling time, with both contaminated groups showing significantly longer handling times.

A precise method for quantifying feeding of *C. maenas* in polluted sediments, using the polychaete *Hediste* (*Nereis*) *diversicolor* as food, was developed (Moreira et al. 2006b). Organisms were deployed at several reference and contaminated sites, and reduced feeding (16.3–72.7 %) was observed at all contaminated sites.

Litter

Marine debris can become part of the diet of animals. Small plastic fragments are available to invertebrates because they are in the same size range as their normal food items. Many of these small fragments come from fishing debris, which accumulates in areas used by commercially important marine life. Of 120 specimens of Norway lobster, *Nephrops norvegicus* collected from the Clyde Sea, Scotland, 83 % contained plastic in their stomachs. This plastic consisted mainly of monofilament strands of different colors and thickness (Murray and Cowie 2011). *Nephrops* fed fish seeded with strands of polypropylene rope were able to ingest but not to excrete the strands. The study showed that some filaments are unable to pass through the gastric mill system (composed of one median and two serrated lateral teeth) and into the pyloric stomach for eventual elimination via the hindgut. The long-term effects of this build-up are unknown and should be investigated.

2.1.2 Mollusks

Mollusks also reduce their feeding activity after exposure to a variety of toxicants. Shipp and Grant (2006) and Krell et al. (2011) developed a short-term in situ toxicity assay based on the post-exposure feeding of the mudsnail *Hydrobia ulvae*. Growth

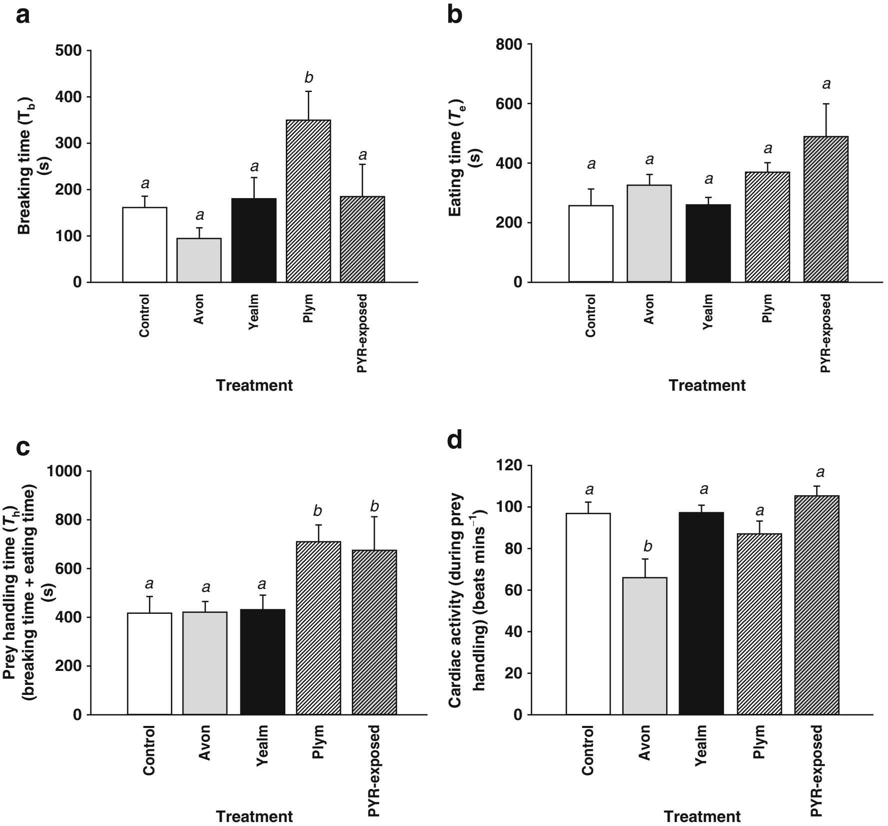

Fig. 2.3 Foraging behaviours (mean + SE) in adult *Carcinus maenas*. (**a**). Breaking time of shelled prey, (**b**) eating time of flesh, (**c**) handling time, and (**d**) cardiac activity during prey handling time (beats/min). *Different letters* = significant differences (Reprinted from Dissanayake et al. 2010, 70: 368–373, 73: 96, courtesy of Elsevier Publishing Co)

over 28 days in *H. ulvae* was reduced at all sites where other studies had detected adverse ecological effects. Feeding rate after 24 h also was decreased at moderately contaminated sites where sediments were not acutely toxic, and feeding was a very good predictor of 28-day growth. Methodologies to quantify post-exposure egestion as a surrogate of feeding were also developed. Reduced feeding in these bioassays was a good predictor of growth.

Metals

Feeding behavior of snails and bivalves has been analyzed in the presence of metal contaminants. Filtration rates of the mussel *Mytilus edulis* and clam *Mya arenaria* were reduced by exposure to chromium (1 mg l^{-1}), to sediments from a

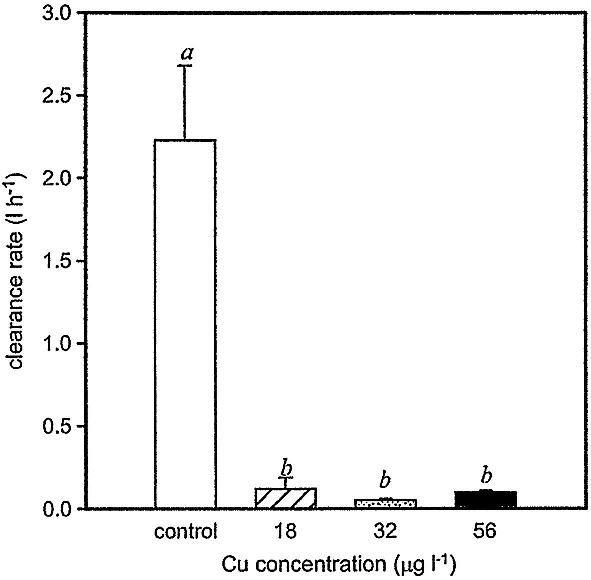

Fig. 2.4 Clearance rates (M ± SE) of *M. edulis* following 5 days exposure to copper. *Different letters* = significant differences (Reprinted from Al-Subiai et al. 2011: 1916, reprinted courtesy of Elsevier Publishing Co)

Cr-contaminated site, or to artificial sediments enriched in Cr (Capuzzo and Sasner 1977). Both dissolved and particulate Cr ($CrCl_3$) reduced filtration rates; *Mya* was less affected than *Mytilus* by particulate Cr. *M. edulis* were exposed for 5 days to Cu (18–56 μg l^{-1}). While molecular biomarkers were affected at 56 μg l^{-1} Cu, the clearance rate showed a significant decrease at concentrations of 18 μg l^{-1} (Fig. 2.4) (Al-Subiai et al. 2011), supporting previous observations that feeding is more sensitive than biochemical biomarkers.

Mollusks are particularly sensitive to copper, which is used as a molluscicide. Effects of 20 μg Cu^{2+} l^{-1} and lowered salinity (20 psu) were studied on the grazing snail *Trochus maculatus* and the macroalgae, *Gracilaria tenuistipitata* and *Enteromorpha intestinalis* (Elfwing and Tedengren 2002). The two factors were applied both separately and in combination to evaluate interactions. Results indicated that moderate salinity reduction and ecologically relevant amounts of Cu reduced snail grazing but not algal productivity, and thus could promote algal growth and potential dominance on coral reefs.

Organics

Oil and Dispersants

Exposure of mussels (*M. edulis*) to an unresolved complex mixture (UCM) of aromatic hydrocarbons isolated from crude oil reduced feeding rate by 40 %

(Donkin et al. 2003). The feeding rate of mussels collected from polluted sites increased when they were placed in clean water, suggesting depuration of toxicants. Water into which mussels from an oil-polluted site had depurated contained a UCM, and tissue extracts of mussels from polluted sites reduced the feeding activity of juvenile mussels. Extracts of mussels from an oil-polluted site were fractionated by HPLC, and a fraction comprising a monoaromatic UCM, reduced feeding of juvenile mussels by 70 %.

Since dispersants are often used following oil spills, there is concern that they may exert toxic effects. The objective of dispersant use is to increase the amount of oil that mixes into the water column, reducing the chances that a slick will contaminate the shoreline or come into contact with birds, marine mammals, or other organisms on the surface or shoreline. By promoting dispersion into the water, however, dispersants increase the potential exposure of biota to both oil and the dispersants themselves. Feeding rates of *M. edulis* exposed to two common oil dispersants were measured by Scarlett et al. (2005). Effects were assessed at dispersant concentrations of 50 mg^{-1} for 48 h. Feeding was reduced dramatically by both dispersants, with SD-25 reducing feeding to 9.8 % of control levels and Corexit® 9527 reducing feeding rates to only 2.6 % of controls.

Pesticides

Filtration rate of adult Pacific oysters *Crassostrea gigas* in response to different concentrations of lindane (gamma-hexachlorocyclohexane [γ-HCH]) for 12 days was investigated (Anguiano et al. 2007). Oysters were exposed to ten different concentrations (<10.0 mg l^{-1}) of γ-HCH. After 4 h of exposure to 0.3 and 0.7 mg l^{-1} γ-HCH, filtration rates were reduced compared with controls to 65.8 and 38.2 %, respectively. After 11 days of exposure, filtration rates were reduced to 60.4 and 30.9 % at concentrations of 0.1 mg l^{-1} and higher. This study showed the filtration rate to be more sensitive than genotoxicity and cytotoxicity.

Hypoxia

Significant differences were noticed in the feeding rate of the oyster drill *Stramonita haemastoma* exposed to hypoxia. Feeding rate in *S. haemastoma* declined linearly with declining oxygen concentration (Das and Stickle 1993).

Contaminants of Emerging Concern

Since mussels take up 100-nm polystyrene (PS) beads, effects of 30-nm PS on the feeding behavior of the blue mussel (*M. edulis*) were studied by Wegner et al. (2012) by exposing mussels to different nano PS and different concentrations of algae (*Pavlova lutheri*). In all treatments, mussels produced pseudofeces. Mussels reduced their filtering activity when nano PS was present, but still reduced the nano

PS concentration in the water and accumulated it. Authors felt that chronic effect studies are needed to further investigate effects of nanoplastics on *M. edulis* and possible consequences for its predators.

Polluted Sites

Growth in *Hydrobia ulvae* was reduced at metal-contaminated field sites, which was associated with reduced feeding rates. Feeding rate after 24 h also was decreased at moderately contaminated sites, which was a very good predictor of 28-day growth (Shipp and Grant 2006).

2.1.3 Fishes

Fish feeding, like that of crustaceans and mollusks, is generally reduced after exposure to a variety of contaminants. These responses are discussed in greater detail under "prey capture" in the behavior chapter.

Metals

Weis and Khan (1990) found that exposure of adult mummichogs (*F. heteroclitus*) to 10 $\mu g\ l^{-1}$ of either $HgCl_2$ or meHg for 1 week reduced feeding rate. In addition, feeding of mummichog larvae was examined after embryonic exposure to 5 or 10 $\mu g\ l^{-1}$. After hatching, larvae were maintained in clean water. Feeding by early larvae was reduced by the embryonic exposure, but approximately 1 week after hatching feeding was comparable to controls, showing that this effect was temporary (Weis and Weis 1995a). The exposure may have caused retardation of neurological development that was subsequently compensated for. After exposure during both embryonic and larval stages, deleterious effects on feeding were greater than after embryonic exposure alone, i.e. lower concentrations were seen to reduce feeding (Zhou et al. 2001).

Organics

Embryonic exposure of mummichogs to environmentally relevant concentrations of PCBs similarly reduced prey capture of larvae (Couillard et al. 2011). The lowest observed effective dose was 5.0 pg PCB126 egg^{-1}. Prey capture efficiency (number of *Artemia* captured per feeding strike) was reduced at ≥ 10.0 pg egg^{-1}. In microcosm experiments, juvenile spot (*Leiostomus xanthurus*) removed fewer harpacticoid copepods from PAH-contaminated sediments than from reference sediments (Marshall and Coull 1996). This may reflect avoidance of the contaminated sediments or a decreased feeding response due to toxicity.

Acidification

Nowicki et al. (2012) found CO_2 level did not significantly affect foraging in juvenile anemonefish, but there was an interaction with temperature. At high temperature (31.5 °C) and control or moderate (530 μatm) CO_2 food consumption and foraging activity were reduced, while high temperature and high CO_2 (960 μatm) increased feeding. Maintaining food consumption and foraging activity in high temperature and CO_2 may reduce energy efficiency if the thermal optimum for food assimilation and growth has been exceeded. The authors concluded that the interaction of rising temperatures and CO_2 will have deleterious effects on this species by mid-century.

Contaminants of Emerging Concern (CECs)

Feeding was inhibited by the anti-depressant fluoxetine, (a selective serotonin reuptake inhibitor, SSRI) in hybrid striped bass (*Morone saxatilis* x *M. chrysops*)., with significant effects observed after only 6 days at the lowest concentration, 23.2 μg l^{-1} (Gaworecki and Klaine 2008). Increased time to capture food was correlated with decreases in brain serotonin activity, which also decreased in a time- and concentration-dependent manner.

Hypoxia

Growth rates of both winter flounder *Pseudopleuronectes americanus* and summer flounder *Paralichthys dentatus* were generally reduced as DO decreased, particularly at DO levels of 50–70 % air saturation, and as temperature increased (Stierhoff et al. 2006). Summer flounder were more tolerant of low DO than winter flounder in this laboratory experiment. A significant relationship between feeding rate and growth indicated that reduced feeding was the major cause of growth reduction. Effects of moderate hypoxia and oscillating DO on feeding and growth of European sea bass (*Dicentrarchus labrax*) were investigated (Thetmeyer et al. 2001). Fish were exposed to one of three oxygen regimes (40 % air saturation; oscillations between 40 and 86 % with a period of 770 min; 86 % as a control) for 1 month. Fish in hypoxia consumed less food, had reduced growth, and a lower condition factor. Fish in oscillating conditions were intermediate. Growth was correlated with food intake, suggesting that reduced growth is primarily due to reduced appetite. Juvenile turbot *Scophthalmus maximus* were fed to satiation at O_2-concentrations of 3.5, and 5.0 mg l^{-1} and 7.2 mg l^{-1} (normoxia) (Pichavant et al. 2000). Both food intake and growth were significantly lower under reduced DO. During the first 2 weeks of the experiment, food intake was halved in hypoxic conditions, and there were large differences among treatments in feed conversion ratio. When juvenile turbot, *Scophthalmus maximus,* and European sea bass, *Dicentrarchus labrax,* were fed to satiation, food intake and growth were depressed under hypoxia (3.2 and

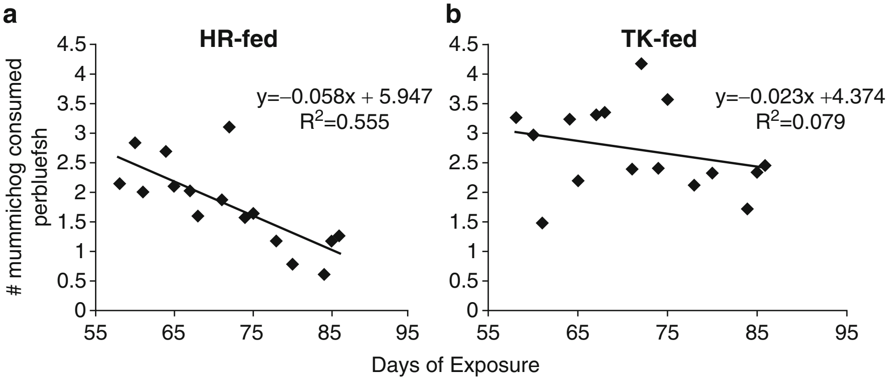

Fig. 2.5 Mean number of mummichogs consumed per bluefish for each trial. (**a**). HR-fed (polluted site) regression analysis ($p = 0.001$). (**b**). TK-fed (reference) regression analysis ($p = 0.291$) (Reprinted from Candelmo et al. 2010: 1031, courtesy Springer Publishing Co)

4.5 mg O_2 l^{-1}) (Pichavant et al. 2001). Growth was comparable between fish in hypoxia that were fed to satiation and fish in normoxia that were fed restricted rations. Decreased food intake is a mechanism by which prolonged hypoxia reduces growth, and may be a way to reduce energy and oxygen demand under hypoxic conditions.

Negative effects of hypoxia on fish feeding can sometimes be compensated for by increased availability of benthic prey during periods of hypoxia. For example, in a field study, spot (*Leiostomus xanthurus*) and hogchoker (*Trinectes maculatus*) showed evidence of optimal prey exploitation during or right after hypoxic events in Chesapeake Bay (Pihl et al. 1992). In most instances gut contents contained larger, deeper-burrowing prey during periods of low oxygen than during normal oxygen levels. Spot consumed a greater biomass (45–73 %) of polychaetes than other prey, with crustaceans initially also constituting a main dietary component. The deep-burrowing anemone, *Edwardsia elegans*, was an important prey species for spot, particularly in deeper hypoxic areas. Prey consumed by 10-to 15-cm-long spot increased significantly in size during some hypoxic events, suggesting a sublethal effect of hypoxia causing large benthic species to move up closer to the sediment surface where they are more available to fish predators.

Polluted Environment

Young-of-the-year bluefish *Pomatomus saltatrix*, that were fed diets in the laboratory of contaminated food (mummichogs and menhaden from Hackensack Meadowlands, an estuary with multiple contaminants including Hg and PCBs), gradually showed reduced appetite and consumed less food than fish that had been fed diets of the same species from a reference estuary (Candelmo et al. 2010) (Fig. 2.5). Bluefish fed contaminated diets grew more slowly, probably due to the reduced food intake.

2.1.4 Other Taxa

Metals

Coral feeding on zooplankton can be inhibited by metal exposure. Peng et al. (2004) found that Cu-exposed corals, *Subergorgia suberosa* were unable to catch or consume brine shrimp effectively. The rate of successful feeding for control polyps was 85 %, but was 57 % at 0.2 μg Cu l^{-1} and only 24 % at 0.5 μg Cu l^{-1}. This is one of the most sensitive responses to Cu. Other metals (Zn, Cd, Pb) did not produce this sublethal effect.

Organics

The deposit feeding lugworm, *Arenicola cristata*, exposed to Kepone (>2.8 μg l^{-1}) showed a significant reduction in sediment processing (feeding) (Rubenstein 1979). The reduction of sediment reworking by these deposit feeders could affect sediment-water column dynamics and alter benthic food chains.

Effects of oil on the sea anemone *Actinia equina* were investigated by Ormond and Caldwell (1982). After 7 weeks exposure to 2.5 ml l^{-1} crude oil, anemones were frequently observed with tentacles expanded and mouth open, but the response to food offered to the tentacles was slow or absent. In separate tests it was found that crude oil presented on filter paper to the anemones could act as a feeding inducer, but that it interfered with or diluted the action of natural feeding inducers present in fish muscle extract.

Corals normally acquire food by a combination of filter feeding by the tentacles of the polyps at night and by photosynthesis by the symbiotic dinoflagellates (zooxanthellae) in cells lining the polyp's gut during the day. When filter feeding, tentacles capture planktonic prey, which are stunned or killed by the nematocysts on the tentacles. Corals also produce mucus, which can trap planktonic prey. Dinoflagellates in the genus *Symbiodinium* occur as endosymbionts, forming a mutualistic relationship with their coral host (Baker 2003). They provide the coral with fixed carbon for energy, remove waste products, and enhance calcification. The host coral polyp provides its zooxanthellae with protection and with carbon dioxide and nutrients in its waste that can be used for photosynthetic processes. This symbiotic relationship allows corals to thrive because of the tight coupling of resources and the advantage of combining filter feeding at night and algal photosynthesis in the day. However, the relationship can be disrupted by a number of stresses, including various pesticides. Irgarol is now used in antifouling paints as a substitute for tributyltin, which has been banned in many countries. Irgarol 1051 was detected by Owen et al. (2002) in marinas, harbors and coastal waters of Florida, Bermuda and St. Croix, with concentrations ranging between 3 and 294 ng l^{-1}. Incubation experiments with isolated zooxanthellae from the coral *Madracis mirabilis* showed no incorporation of $H^{14}CO_3^-$ from seawater (no photosynthesis) after 4–8 h exposure to Irgarol 1051 concentrations as low as 63 ng l^{-1}. Reduction in net photosynthesis of intact corals was found at concentrations of 100 ng l^{-1} with little or no photosynthesis at concentrations exceeding 1,000 ng l^{-1} after 2–8 h exposure. These data suggest Irgarol 1051 is prevalent in tropical marine ecosystems and is a potent inhibitor of coral photosynthesis at environmentally relevant concentrations.

Similarly, Photosystem II (PSII) herbicides used in agriculture and antifouling paints can affect corals and their symbiotic dinoflagellates. Jones (2006) reviewed ecotoxicological studies and found that PSII herbicides readily penetrate coral tissues and within minutes reduce the photochemical efficiency of the algal symbionts, with photosynthesis being affected at low concentrations (i.e. in the ng l^{-1} range). At these levels and over short exposure periods, effects are reversible when corals are returned to clean seawater. However, with higher concentrations or longer exposure periods, there is long-term reduction of the photochemical efficiency of the algae, which can result in the loss of the symbionts (bleaching, see below) a stress response that requires months for recovery.

Markey et al. (2007) investigated various pesticides for effects on the coral *Acropora millepora*. Most had few visible effects on adults after 96 h exposure to 10 μg l^{-1}, with the exception of profenofos, which caused polyp retraction, bleaching, and a slight reduction in photosynthetic efficiency of the algal symbionts. The fungicide MEMC (2-methoxyethylmercuric chloride) caused polyps to become withdrawn and photosynthetic efficiency was slightly reduced at 1.0 μg l^{-1}. At 10 μg l^{-1} MEMC, branches bleached and some host tissue died.

Climate Change

Corals

The symbiotic relationship of corals and zooxanthellae is vulnerable to stresses such as elevated temperature, which causes the corals to bleach, i.e. lose their zooxanthellae (see Fig. 1.9). While bleaching can also be caused by intense irradiance, chemical stresses (see above), freshwater inflow, and sedimentation, elevated temperature is the primary cause of mass bleaching events (Kleppel et al. 1989). Most reef-building corals normally contain around $1–5 \times 10^6$ zooxanthellae cm^{-2} of live surface tissue and 2–10 pg of chlorophyll *a* per zooxanthella. Photosynthetic pathways in zooxanthellae are impaired at temperatures above 30 °C, which could activate the separation of coral and algae. When corals bleach they generally lose 60–90 % of their zooxanthellae and each remaining zooxanthella may lose 50–80 % of its photosynthetic pigments (Glynn 1996). The pale appearance of bleached corals is due to the calcareous skeleton showing through the tissues that have lost pigmented zooxanthellae. Temperature shocks can also reduce zooxanthellae through loss of cell adhesion, the detachment of coral endodermal cells from their zooxanthellae and eventual expulsion. If bleaching is not too severe and if it decreases over time, the corals may regain their symbiotic algae within several weeks or months. If zooxanthellae loss continues and dinoflagellate populations do not recover, the coral eventually dies because filter feeding is not adequate to meet its nutritional needs. However the coral plays a significant role in recovery and resilience, and some species can adjust. Bleached and recovering *Montipora capitata* corals could meet all their daily metabolic energy requirements by increasing their feeding rates and CHAR (percent contribution of heterotrophically acquired carbon to daily animal respiration), whereas *Porites compressa* and *Porites lobata* could not. Therefore coral species with high-CHAR capability are more resilient to bleaching, and may become the dominant coral species on reefs in the future (Grottoli et al. 2006).

It had been hoped that corals living inside marine protected areas (MPAs) where there is no fishing would also be more resilient to effects of increased temperatures. To determine whether coral deaths caused by bleaching were lower inside MPAs, Selig et al. (2012) compared over 8,000 coral reef surveys by divers with satellite measurements of ocean surface temperatures. They found that although MPAs could help coral populations recover from temperature-induced mortality in some situations, it did not appear to be a general solution. In general, corals living inside MPAs were just as susceptible to warming as unprotected corals.

While there is some specialization of particular hosts for particular *Symbiodinium* species, many corals associate with more than one type of *Symbiodinium*, and a particular *Symbiodinium* may associate with a variety of hosts (Baker 2003). This flexibility allows corals to function well in different settings (e.g., shallow, high-light situations versus deep water low-light conditions). Physiologically distinct lines of *Symbiodinium* may have different thermal tolerance. Oliver and Palumbi (2011) found that the coral–algal symbiosis adapts to particular temperature environments through changes in the algal symbiont. It has been hypothesized that bleaching allows the coral to be repopulated with zooxanthellae that are more temperature-resistant. Thus, the coral/algal association may be able to adapt within a coral's lifetime. Corals in warmer environments tend to host *Symbiodinium* that are more thermally tolerant.

Sponges

Elevated temperature also affects feeding in sponges. Massaro et al. (2012) examined the effects of thermal stress on feeding in the Great Barrier Reef sponge, *Rhopaloeides odorabile*, focusing on filtration efficiencies and choanocyte chamber characteristics. When temperature reached 31 °C, flow rate, filtration efficiency, and choanocyte chamber density and size were reduced, thus reducing food intake.

Echinoderms

Acidification altered feeding and growth in sea stars *Asterias rubens* exposed to 650, 1,250 and 3,500 μatm. Appelhans et al. (2012) exposed both the predators and their prey, the blue mussel *Mytilus edulis*, over 10 weeks and subsequently performed feeding assays. Intermediate acidification levels had no significant effect on growth or consumption, but produced a slight increase in feeding and growth. The highest acidification level reduced feeding and growth rates by 56 %. Mussels exposed to elevated pCO_2 were preferred by previously untreated *A. rubens.* A trend toward a lower shell mass in mussels in increasing seawater pCO2 was observed, and the breaking resistance of shells was significantly lowered by ~20 % at 3,500 μatm. Despite the decrease in the breaking resistance of the shell, mussels did not become more susceptible to crab predation under high acidification levels, even though crabs consume them by breaking the shells. Breaking the shell is not the feeding mode of the sea star, which pries open the valves; however, the mussel's adductor muscle (which holds the shells together) was not affected by the acidification. Thus, the altered predation by the sea star predators is not explained by the physical changes (or lack thereof) in the mussels.

Hypoxia/Nutrients

Benthic polychaetes have variable tolerance to low DO. *Loima medusa*, a common species in estuarine habitats where summer hypoxic events often occur can tolerate anoxia or severe hypoxia (7 % air saturation at 26 °C) for 3–5 days (Llanso and Diaz 1994). Under low DO ($<$14 % air saturation) feeding stops, although tube irrigation continues and periodic protrusions from the tube are common. Most worms come out to the sediment surface. The prevalence of *L. medusa* in deep estuarine channels may be partially explained by its tolerance to prolonged periods of hypoxia.

Excess nutrients (N), rather than hypoxia, can affect the susceptibility of corals to bleaching. Increased dissolved inorganic nitrogen (DIN) has been linked to a reduction of the temperature threshold of coral bleaching. Wiedenmann et al. (2013) found that increased DIN and decreased phosphate increased the susceptibility of corals to bleaching. Analyses suggested that the imbalanced supply of DIN results in phosphate starvation of the symbiotic algae. A model was developed that assumes that a transition of zooxanthellae from a nutrient-limited to a nutrient-starved (in this case phosphate) state leads to changes in the lipid composition of the algal membranes. Under stress, the altered photosynthetic membranes and photosystems would impair photosynthesis and cause the breakdown of the symbiosis and loss of zooxanthellae. These results suggest that a balanced reduction of N input in coastal waters could help mitigate effects of increasing temperatures on coral reefs.

Other Cnidarians (e.g. jellyfish) appear to be quite tolerant of low DO, which can give them an advantage over more sensitive taxa. Low DO ($\sim$2 mg l^{-1}) greatly increased predation on fish larvae (naked goby *Gobiosoma bosc*) by sea nettles (*Chrysaora quinquecirrha*) but decreased predation by juvenile striped bass (*Morone saxatilis*) (Breitburg et al. 1997). Predation by the sea nettle increased for fish larvae, decreased for fish eggs, and was not strongly affected for copepods (mostly *Acartia tonsa*) at low DO. Changes in predator–prey interactions reflected species differences in tolerance to low DO and its effects on escape behavior of prey and on swimming and feeding behaviors of predators. Because of the variation in effects, low DO has the potential to alter the relative importance of different pathways of energy flow in estuarine systems. Larvae of the red sea bream *Pagrus major* in four size classes were used as prey in a short-term predation experiment with moon jellyfish *Aurelia aurita*. No change in the bell contraction rate of the jellyfish was observed at the DO levels tested (1, 2 and 4 mg/l, and 5.5–6.0 mg/l), suggesting tolerance to low DO (Shoji et al. 2005). Over 80 % of the 2.5 and 4.1-mm larvae were eaten at all DO concentrations during 15-min trials. The 6.2 and 8.6-mm larvae were able to escape due to their developed swimming ability at the two higher DO concentrations, but they suffered increased predation at the two lower DO levels. Similarly, ctenophores (comb jellies) also are quite tolerant of hypoxia. Laboratory clearance rates of *Mnemiopsis leidyi* feeding on bay anchovy (*Anchoa mitchilli*) eggs and yolk sac larvae, and naked goby (*Gobiosoma bosc*) larvae were as high at low DO (1.5 mg l^{-1}) as at high DO concentrations (7 mg l^{-1}) (Kolesar et al. 2010). Years of field sampling at two sites revealed that ctenophore densities remained high in the bottom even at low DO levels.

Polluted Sites

Sediments from estuaries in Southwest Portugal classified as undisturbed and impacted were tested on the polychaete *Hediste diversicolor* (Moreira et al. 2006a). A significant depression in post-exposure feeding (from 30 to 70 %) was consistently seen in all impacted sediments, supporting the sensitivity and responsiveness of feeding as a sublethal endpoint. Along with a reduced energy intake, increased anaerobic metabolism (enhancement of lactate dehydrogenase activity), suggested a rapid need for additional energy to ameliorate chemical stress.

This section has shown that reduced feeding (or reduced energy uptake from photosynthetic symbionts) is a very common response to a variety of pollutant stresses. Reduced energy intake can be the initial impetus for a variety of subsequent responses, including respiration, growth, etc. that will be discussed in subsequent chapters.

2.2 Digestion and Assimilation

Ingested pollutants can alter digestive physiology even before they are assimilated – while still in the gut fluids they can affect gut motility, enzyme activities, or absorption (De La Ruelle et al. 1992). This is termed “pre-assimilatory toxicity.” Post-assimilatory toxicity occurs after the pollutant has been incorporated into tissues; this may damage gut tissues and interfere with digestive enzyme synthesis or release, and interfere with absorption, transport and subsequent assimilation of nutrients (and pollutants), and thus impact energy reserves (Seebaugh 2010). Most studies, however, do not attempt to distinguish between pre- and post-assimilatory toxicity. Impacts on digestive function may depend on the manner of exposure.

2.2.1 Crustaceans

Metals

Digestive enzymes tend to be inhibited by metals (Li et al. 2008). Sarojini et al. (1992) reported that amylase, lipase, and protease activities of the stomach, midgut, and hindgut of the prawn *Caridina rajadhari* were reduced after exposure to tributyltin. Cd exposure (0.05 mg l^{-1}) reduced food assimilation efficiency and fecal pellet production in the mysid *Leptomysis* (Gaudy et al. 1991). Exposures ranged from 0.01 to 0.2 mg l^{-1}. Reduced food intake, combined with decreases in fecal pellet production and reduced assimilation efficiency reflected a significant decrease in energy which authors felt would lead to an unbalanced energy budget and lower reproductive potential. Hydrolase activity increased initially at 0.2 mg Cd l^{-1}, but after 48 h it declined, reaching very low values at 72 h. The unbalanced energy budget was an overall consequence of the inability to utilize food.

Cd in prey altered assimilation efficiency of Cd in the grass shrimp, *P. pugio* (Seebaugh and Wallace 2004; Seebaugh et al. 2006). Cd assimilation was positively correlated with gut residence time in shrimp collected along a pollution gradient. Increased gut residence time can, in turn, influence pollutant assimilation. Ingestion of a pulse of Cd reduced protease activities and fecal elimination rate (Seebaugh 2010). Digestive protease activities could have been influenced by pre-assimilatory interactions between Cd in the gut fluids and enzyme-secreting cells, or they could have resulted from impacts on stored or circulating enzymes. Ingestion of a pulse of Cd can influence protease activities and fecal elimination rate (Seebaugh 2010). Thus, previous exposure to dietary metals can induce changes in digestive physiology and affect digestive enzymes that may influence future digestion and assimilation.

Grass shrimp fed Cd-containing polychaetes did not show a change in carbon assimilation efficiency, minimum gut residence time, or gut pH, but did show a dose-dependent decrease in feces elimination rate and an increase in protease activities, but the latter was not dose-dependent (Seebaugh et al. 2012a). Studies with dye-labeled food suggested that the reduced feces elimination rate was not due to reduced food intake, but rather to reduced feces packaging and transport, possibly by affecting the muscles responsible for peristalsis.

Grass shrimp were fed Hg-contaminated oligochaetes (*Tubifex* worms exposed to 0.007, 0.014, or 0.028 lM Hg for 96 h) over a 15-day period and analyzed for Hg, Cd, and carbon assimilation efficiencies (AE) as well as end points related to digestion (Seebaugh et al. 2012b). Hg AE by pre-exposed shrimp reached a plateau (approximately 53 %), whereas Cd AE varied (approximately 40–60 %) in a manner that was not dose-dependent. Carbon AE did not differ among treatments. Gut residence time and feces elimination were not impacted. Extracellular protease activity varied but did not exhibit dose-dependency. pH increased over the range of Hg pre-exposures within the gut, and Hg assimilation had a negative relationship to hydrogen ion concentrations. Thus, previous Hg ingestion can elicit post-assimilatory impacts on digestive physiology, which may, in turn, influence subsequent Hg assimilation.

Organic Pollutants – Pesticides

There have been few studies on effects of organic pollutants on digestion. Fisher and Clark (1990) examined kepone and assimilation in grass shrimp, *P. pugio*. Grass shrimp and their food were exposed to a Kepone concentration of 0.04 $\mu g\ l^{-1}$. A first-order pharmacokinetic equation was used to model accumulation kinetics during 16-day uptake and 21-day clearance. Doubling the contaminated food ration caused a significant increase in the whole-body Kepone concentration. Shrimp fed either a 4 or 8 % ration of uncontaminated food and exposed to Kepone in water bioconcentrated Kepone equally. When shrimp were exposed to contaminated water and food, Kepone accumulation from each source was additive, but the food was very important in determining final body burdens. Dietary Kepone represented approximately 24 and 33 % of the total body burden accumulated by shrimp fed 4 and 8 % food rations, respectively, but assimilation efficiencies of Kepone from the food were low.

Horst et al. (2007) found that exposure to the juvenile hormone analog methoprene (50 $\mu g\ l^{-1}$) caused up-regulation of genes in the hepatopancreas of the lobster, *Homarus americanus*, for the enzymes betaine-homocysteine *S*-methyltransferase (BHMT) and other enzymes of the methionine cycle. Increased levels of enzymes associated with protein turnover, including trypsin, ubiquitin conjugating enzyme, and ubiquitin carboxyl terminal hydrolase were also observed.

Polluted Sites

Grass shrimp (*P. pugio*) from polluted sites had reduced digestive protease activity compared to shrimp from a reference site. Casein hydrolysis rates were negatively correlated with gut residence time and inversely related to AE of Cd (Seebaugh 2010), which would affect future assimilation of pollutants. However, carbon assimilation was not affected, suggesting that the shrimp could compensate for metal-induced post-assimilatory toxicity to maintain assimilation of nutrients (Seebaugh 2010). It appears that gut plasticity (increasing gut residence time) allows shrimp in contaminated sites to maintain adequate assimilation of essential nutrients, but may increase the risk of dietary exposure to specific pollutants. There was a trend of increasing gut residence time with increasing dietary Cd but not Hg or carbon. Increased gut residence time can compensate for reduced digestive enzyme activities. Fecal elimination rate was also not affected by field exposure, which also may be a compensatory response to impacts of pollutants. Seebaugh et al. (2011) found that digestive protease activities decreased markedly in grass shrimp from impacted field sites relative to reference shrimp, and suggested that digestive plasticity (increasing gut residence time) may be important in compensating for post-assimilatory digestive toxicity (reduced protease activities) in order to maintain nutrient assimilation. Stress-induced variability in digestive function may, in turn, enhance the assimilation of non-essential elements, such as Cd.

2.2.2 Mollusks

Pesticides

Field-collected oysters, *C. gigas* from areas in Northwest France highly contaminated with urea herbicides showed elevated mortality. Laboratory exposures to diuron and isoproturon, 0.5 and 1 μ gl^{-1} produced histopathology in the digestive system (atrophy of the digestive tubule epithelium) (Buisson et al. 2008), which would affect digestion and assimilation.

Contaminants of Emerging Concern

Canesi et al. (2012) exposed mussels (*M. edulis*) to nanoparticles (NPs) and found that, due to the physiological mechanisms involved in the feeding process, NP agglomerates/aggregates taken up by the gills were directed to the digestive gland, where intracellular uptake of nanosized materials induced lysosomal perturbations and oxidative stress. This could be a major mechanism of action underlying the potential toxicity of NPs in marine invertebrates.

Acidification

Juvenile *Mytilus galloprovincialis* under conditions of −0.3 and −0.6 pH units for 78 days showed increased absorption efficiency and ammonium excretion, and increased scope for growth and tissue dry weight, suggesting that this species is tolerant to acidification (Fernandez-Reiriz et al. 2012). Feeding itself was unaffected.

2.2.3 Fishes

Metals

Socci and Farmanfarmaian (1985) investigated effects of inorganic Hg, methylmercury, and Cd (<5.0 mg l^{-1}) on intestinal absorption of amino acids (l-leucine and l-methionine) by the toadfish, *Opsanus tau*, using an *in vitro* system. At 2.5 mg l^{-1} inorganic Hg inhibited leucine uptake, while meHg inhibited uptake at 5 mg l^{-1}. For methionine, inorganic Hg reduced intestinal uptake at 5 mg l^{-1}, while meHg inhibited it at 2.5 mg l^{-1}. It is of interest that for leucine, $HgCl_2$ was a more potent inhibitor of intestinal uptake, which is unusual, in that meHg is generally the more toxic form of the metal.

A high concentration (6.8 mg l^{-1}) of Cd affected the histology and enzyme activities of the alimentary tract and liver of the fish, *Heteropneustes fossilis* (Sastry and

Gupta 1979). Three phosphatases studied were significantly inhibited in the liver and intestine. Pepsin activity was elevated in the stomach, but trypsin was inhibited in the intestine. Inhibition was also noted in the activities of aminotripeptidase and glycylglycine dipeptidase. High concentrations (0.3 mg l^{-1}) of $HgCl_2$ also affected digestive enzymes in this fish (Gupta and Sastry 1981). The activities of alkaline phosphatase and glucose-6-phosphatase decreased, while acid phosphatase activity was elevated above normal. Significant decreases were observed in activities of all the digestive enzymes except pepsin.

These experiments are decades old, and used high concentrations of metals, well above those encountered in the field; thus, there is a need for new studies on effects of lower levels of contaminants on fish digestive and assimilative activities.

Organic Pollutants – Pesticides

DDT exposure (0.05 or 0.1 mg l^{-1} for 24 h) of mummichogs (*Fundulus heteroclitus*) impaired intestinal absorption of amino acids (Miller and Kinter 1977). The authors thought this was due to impairment of membrane transport and speculated that this could lead to reduced nutrition and growth.

Hypoxia

Juvenile cod (*Gadus morhua*) were exposed to low DO to investigate digestion and metabolism (Jordan and Steffenson 2007). Reduced oxygen (6.3 kPa PO_2) depressed the usual postprandial (after feeding) increase in oxygen consumption. The specific dynamic action (production of heat associated with the ingestion of food) lasted over twice as long, perhaps to compensate for the reduced oxygen availability. The percentage of energy associated with digestion and assimilation was greater in hypoxia, occupying most of the scope for activity and leaving little energy for other activities On the other hand, postprandial blood flow to the gut during hypoxia was not proportionately reduced in sea bass, as predicted by Axelsson et al. (2002). Although post-prandial absolute blood flow decreased during hypoxia, the relative proportion of cardiac output reaching the gut did not decrease. This was unlike the situation in non-feeding fish.

2.2.4 Other Taxa

Metals

Chen et al. (2002) assessed potential impacts of Cu on digestive enzyme activities in a wide range of benthic invertebrates (echinoderms, mollusks, polychaetes, echiurids, and hemichordates), by monitoring enzyme activities in their gut fluids during *in vitro* titrations with dissolved Cu, which mimics Cu solubilization from sediments. Increasing Cu inhibited digestive protease activities at values that varied from 8 μM for an echinoderm to 0.4 M for an echiuran. Threshold Cu concentrations were similar for different digestive enzymes, suggesting the same inhibition mechanism. Copper was less effective at inhibiting enzymes at lower pH, suggesting that H^+ can compete with Cu ion for binding to active sites or that enzyme conformation is less vulnerable to Cu inhibition at lower pH. The results suggest that animals with low enzyme activity and high gut pH are more vulnerable to Cu, although they solubilize less sedimentary Cu than animals with high enzyme activity and low gut pH.

Seick et al. (1999) examined how cadmium pre-exposure (3 and 30 μg Cd g^{-1} dry wt. sediment) and gut passage time interact to determine cadmium absorption efficiency (Cd-AE) in the polychaete *Capitella* sp. A 5-day pre-exposure to Cd did not affect egestion rates during either the pre-exposure period or the chase phase. Overall, Cd-AE increased with increasing gut passage time in worms that were not pre-exposed, but pre-exposure to cadmium reversed the relationship between gut passage time and Cd-AE. Thus, worm physiology may be especially important in controlling metal bioavailability in deposit-feeding organisms and should be considered in sediment quality approaches.

Organics

Schweitzer et al. (2000) examined dietary assimilation of PCBs and maternal transfer in sea urchins. Adult *Lytechinus pictus* were allowed to graze on sediment spiked with radiolabeled PCB, 2,2′,4,4′-tetrachlorobiphenyl for 35 days. *L. pictus* was found to have quite high extraction efficiency; approx. 62 % of the PCB sediment concentration was removed while passing through the gut. Maternal transfer was not a more sensitive exposure route to developing embryos than direct water exposure. Both adults and embryos were resilient to this PCB at environmentally relevant sediment concentrations. Low toxicity of PCBs allows for significant bioaccumulation in sea urchins.

Hypoxia

Specific feeding rate, growth, and production efficiency were measured on individuals of the polychaete *Capitella* species 1 to determine whether previously measured declines in growth rates in response to hypoxia were due to decreased feeding, decreased conversion efficiency, or both (Forbes et al. 1994). The relationship between feeding rate and growth was influenced by oxygen concentration such that in relatively nitrogen-poor sediment, greater growth rates were observed at lower DO. Measurements of growth and feeding rates indicated that the effect of DO was due to a decrease in the efficiency with which ingested sediment was converted to tissue under low N, high DO conditions. Authors suggested that the decreased conversion rate of ingested sediment to body volume under the higher DO regime reflected an aerobic metabolic system poised to rapidly exploit available oxygen supplies.

Along with tolerance to hypoxia in their feeding responses, gelatinous taxa also appear to have high tolerance in their digestive processes. Ctenophore (*Mnemiopsis leidyi*) digestion rates were unchanged at oxygen concentrations of 1 mg l^{-1} (Decker et al. 2004). Gelatinous species, which are more tolerant of hypoxia than fishes, may be able to inhabit regions of low oxygen that are avoided by zooplanktivorous fishes that have higher oxygen requirements. This could lead to dominance of gelatinous predators in areas affected by hypoxia and might alter energy pathways in these systems.

Polluted Sites

The polychaete *Nereis diversicolor* from a polluted estuary (Loire) and a relatively clean site (Bay of Bourgneuf) were compared (Kalman et al. 2009). Significant inhibition of the digestive enzymes amylase and carboxymethylcellulase were recorded in individuals from the Loire compared to the reference site. Feeding and egestion rates were also depressed in worms from the Loire compared to the reference site. This impairment was accompanied by changes in digestive enzyme activities, which could explain the generally poorer condition of worms in the Loire estuary.

2.3 Conclusions

Most animals respond to most contaminants with a reduction in feeding and digestion. Decreased food intake places energetic demands on the organism, which may be responsible for decreases in other physiological functions (e.g. respiration) that will be discussed in the following chapters. In many cases when food intake is reduced, animals reduce their activity in order to conserve energy; this in turn may make it harder to find and get food – which intensifies the problem in positive feedback situation. The taxonomic group that would seem to be at greatest risk of mortality from reduced energy intake would appear be the corals, which get most of their energy requirements from their photosynthetic symbionts, which are very sensitive to toxicants and temperature. Coral bleaching can frequently lead to mortality.

References

Al-Subiai N, Moody AJ, Mustafa SA, Jha AN (2011) A multiple biomarker approach to investigate the effects of copper on the marine bivalve mollusc, *Mytilus edulis*. Ecotoxicol Environ Saf 74:1913–1920

Anguiano G, Llera-Herrera R, Rojas E, Vazquez-Boucard C (2007) Subchronic organismal toxicity, cytotoxicity, genotoxicity, and feeding response of pacific oyster (*Crassostrea gigas*) to lindane (γ-HCH) exposure under experimental conditions. Environ Toxicol Chem 26:2192–2197

Appelhans YS, Thomsen J, Pansch C, Melzner F, Wahl M (2012) Sour times: seawater acidification effects on growth, feeding behaviour and acid–base status of *Asterias rubens* and *Carcinus maenas*. Mar Ecol Prog Ser 459:85–98

Axelsson M, Altimiras J, Claireux G (2002) Post-prandial blood flow to the gastrointestinal tract is not compromised during hypoxia in the sea bass *Dicentrarchus labrax*. J Exp Biol 205:2891–2896*

Baker A (2003) Flexibility and specificity in coral-algal symbiosis: diversity, ecology and biogeography of *Symbiodinium*. Annu Rev Ecol Evol Syst 34:661–689

Bell GW, Eggleston DB, Wolcott TG (2003) Behavioral responses of free-ranging blue crabs to episodic hypoxia. II. Feeding. Mar Ecol Prog Ser 259:227–235

Blockwell SJ, Taylor EJ, Jones I, Pascoe D (1998) The influence of fresh water pollutants and interaction with *Asellus aquaticus* (L) on the feeding activity of *Gammarus pulex* (L). Arch Environ Contam Toxicol 34:41–47

Breitburg DL, Loher T, Pacey CA, Gerstein A (1997) Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecol Monogr 67:489–507

Buisson S, Bouchart V, Guerlet E, Malas JP, Costil K (2008) Level of contamination and impact of pesticides in cupped oyster, *Crassostrea gigas*, reared in a shellfish production area in Normandy (France). J Environ Sci Health B 43:655–664

Candelmo A, Deshpande A, Dockum B, Weis P, Weis JS (2010) The effect of contaminated prey on feeding, activity, and growth of young-of-the-year bluefish, *Pomatomus saltatrix*, in the laboratory. Estuar Coast 33:1025–1038

Canesi L, Ciacci C, Fabbri R, Marcomini A, Pojana G, Gallo G (2012) Bivalve molluscs as a unique target group for nanoparticle toxicity. Mar Environ Res 76:16–21

Capuzzo JM, Sasner JJ (1977) The effect of chromium on filtration rates and metabolic activity of *Mytilus edulis* and *Mya arenaria*. In: Vernberg FJ, Calabrese A, Thurberg FP, Vernberg WB (eds) Physiological responses of Marine Biota to pollutants. Academic, New York, pp 225–237

Chen Z, Mayer LM, Weston DP, Bock MJ, Jumars PA (2002) Inhibition of digestive enzyme activities by copper in the guts of various marine benthic invertebrates. Environ Toxicol Chem 21:1243–1248

Couillard CM, Légaré B, Bernier A, Dionne Z (2011) Embryonic exposure to environmentally relevant concentrations of PCB126 affect prey capture ability of *Fundulus heteroclitus* larvae. Mar Environ Res 71:257–265

Das T, Stickle WB (1993) Sensitivity of crabs *Callinectes sapidus* and *C. similis* and the gastropod *Stramonita haemastoma* to hypoxia and anoxia. Mar Ecol Prog Ser 98:263–274

De la Ruelle M, Hajjou M, Van Herp F, Le Gal Y (1992) Aminopeptidase activity from the hepatopancreas of *Procambarus clarkii*. Biochem Syst Ecol 20:331–337

Decker MB, Breitburg D, Purcell JE (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. Mar Ecol Prog Ser 280:163–172

Dissanayake A, Galloway TS, Jones MB (2008) Nutritional status of *Carcinus maenas* (Crustacea: Decapoda) influences susceptibility to contaminant exposures. Aquat Toxicol 89:40–46

Dissanayake A, Piggott C, Baldwin C, Sloman KA (2010) Elucidating cellular and behavioural effects of contaminant impact (polycyclic aromatic hydrocarbons, PAHs) in both laboratory-exposed and field-collected shore crabs, *Carcinus maenas* (Crustacea: Decapoda). Mar Environ Res 70:368–373

Donkin P, Smith EL, Rowland SJ (2003) Toxic effects of unresolved complex mixtures of aromatic hydrocarbons accumulated by mussels, *Mytilus edulis*, from contaminated field sites. Environ Sci Technol 37:4825–4830

Elfwing T, Tedengren M (2002) Effects of copper and reduced salinity on grazing activity and macroalgae production: a short-term study on a mollusc grazer, *Trochus maculatus*, and two species of macroalgae in the inner Gulf of Thailand. Mar Biol 140:913–919

Fernandez-Reiriz M, Range P, Alvarex-Salgado X, Espinosa J, Labarta U (2012) Tolerance of juvenile *Mytilus galloprovincialis* to experimental seawater acidification. Mar Ecol Prog Ser 454:65–74

Fisher DJ, Clark JR (1990) Bioaccumulation of Kepone by grass shrimp (*Palaemonetes pugio*): importance of dietary accumulation and food ration. Aquat Toxicol 17:167–186

Forbes TL, Forbes VE, Depledge MH (1994) Individual physiological responses to environmental hypoxia and organic enrichment: implications for early soft-bottom community succession. J Mar Res 52:1081–1100

Gaudy R, Guérin J-P, Kerambrun P (1991) Sublethal effects of cadmium on respiratory metabolism, nutrition, excretion and hydrolase activity in *Leptomysis lingvura* (Crustacea: Mysidacea). Mar Biol 109:493–501

Gaworecki KM, Klaine SJ (2008) Behavioral and biochemical responses of hybrid striped bass during and after fluoxetine exposure. Aquat Toxicol 88:207–213

Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. Glob Change Biol 2:495–509

Grottoli A, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189

Gupta PK, Sastry KV (1981) Effect of mercuric chloride on enzyme activities in the digestive system and chemical composition of liver and muscles of the catfish, *Heteropneustes fossilis*. Ecotoxicol Environ Saf 5:389–400

Horst MN, Walker AN, Bush P, Wilson T, Chang ES, Miller T, Larkin P (2007) Pesticide induced alterations in gene expression in the lobster, *Homarus americanus*. Comp Biochem Physiol Part D Genomics Proteomics 2:44–52

Jensen LK, Carroll J (2010) Experimental studies of reproduction and feeding for two Arctic-dwelling *Calanus* species exposed to crude oil. Aquat Biol 10:261–271

Jones R (2006) The ecotoxicological effects of Photosystem II herbicides on corals. Mar Pollut Bull 51:495–506

Jordan AD, Steffenson JF (2007) Effects of ration size and hypoxia on specific dynamic action in the cod. Physiol Biochem Zool 80:176–185

Kalman J, Palais F, Amiard JC, Mouneyrac C, Muntz A, Blasco J, Riba I, Amiard-Triquet C (2009) Assessment of the health status of populations of the ragworm *Nereis diversicolor* using biomarkers at different levels of biological organization. Mar Ecol Prog Ser 393:55–67

Khoury J, Powers E, Patniak P, Wallace W (2009) Relating disparity in competitive foraging behavior between two populations of fiddler crabs to the subcellular partitioning of metals. Arch Environ Contam Toxicol 56:489–499

Kleppel GS, Dodge RE, Reese CJ (1989) Changes in pigmentation associated with the bleaching of stony corals. Limnol Oceanogr 34:1331–1335

Kolesar SE, Breitburg DL, Purcell JE, Decker MB (2010) Effects of hypoxia on *Mnemiopsis leidyi*, ichthyoplankton and copepods: clearance rates and vertical habitat overlap. Mar Ecol Prog Ser 411:173–188

Krell B, Moreira-Santos M, Ribeiro R (2011) An estuarine mudsnail in situ toxicity assay based on postexposure feeding. Environ Toxicol Chem 30:1935–1942

Li W, Gao K (2012) A marine secondary producer respires and feeds more in a high CO_2 ocean. Mar Pollut Bull 64:699–703

Li N, Zhao Y, Yang J (2008) Effects of water-borne copper on digestive and metabolic enzymes of the giant freshwater prawn *Macrobrachium rosenbergii*. Arch Environ Contam Toxicol 55:86–93

Llanso RJ, Diaz RJ (1994) Tolerance to low dissolved oxygen by the tubicolous polychaete *Loimia medusa*. J Mar Biol Assoc UK 74:143–148

Maltby L, Crane M (1994) Responses of *Gammarus pulex* (Amphipoda: Crustacea) to metalliferous effluents: identification of toxic components and importance of interpopulation variation. Environ Pollut 84:45–52

Markey KL, Baird AH, Humphrey C, Negri AP (2007) Insecticides and a fungicide affect multiple coral life stages. Mar Ecol Prog Ser 330:127–137

Marshall KR, Coull BC (1996) PAH effects on removal of meiobenthic copepods by juvenile spot (*Leiostomus xanthurus*: Pisces). Mar Pollut Bull 32:22–26

Massaro AJ, Weisz JB, Hill MS, Webster NS (2012) Behavioral and morphological changes caused by thermal stress in the Great Barrier Reef sponge *Rhopaloeides odorabile*. J Exp Mar Biol Ecol 416–417:55–60

Miller DS, Kinter WB (1977) DDT inhibits nutrient absorption and osmoregulatory function in *Fundulus heteroclitus*. In: Vernberg FJ, Calabrese A, Thurberg FP, Vernberg WB (eds) Physiological responses of Marine Biota to pollutants. Academic, New York, pp 63–74

Moreira SM, Lima I, Ribeiro R, Guilhermino L (2006a) Effects of estuarine sediment contamination on feeding and on key physiological functions of the polychaete *Hediste diversicolor*: laboratory and in situ assays. Aquat Toxicol 78:186–201

Moreira SM, Moreira-Santos M, Guilhermino L, Ribeiro R (2006b) An in situ postexposure feeding assay with *Carcinus maenas* for estuarine sediment-overlying water toxicity evaluations. Environ Pollut 139:318–329

Murray F, Cowie PR (2011) Plastic contamination in the decapod crustacean *Nephrops norvegicus* (Linnaeus, 1758). Mar Pollut Bull 62:207–1217

Nimmo DR, Hansen DJ, Couch JA, Cooley NR, Parrish PR, Lowe JI (1975) Toxicity of Aroclor® 1254 and its physiological activity in several estuarine organisms. Arch Environ Toxicol Chem 3:22–39

Nowicki JP, Miller GM, Munda PL (2012) Interactive effects of elevated temperature and CO_2 on foraging behavior of juvenile coral reef fish. J Exp Mar Biol Ecol 412:46–51

Oliver TA, Palumbi SR (2011) Many corals host thermally resistant symbionts in high-temperature habitat. Coral Reefs 30:241–250

Ormond RF, Caldwell S (1982) The effect of oil pollution on the reproduction and feeding behaviour of the sea anemone *Actinia equine*. Mar Pollut Bull 13:118–122

Owen R, Knap A, Toaspern M, Carbery K (2002) Inhibition of coral photosynthesis by the antifouling herbicide Irgarol 1051. Mar Pollut Bull 44:623–632

Peng S, Huang J, Xiong T, Huang M (2004) Effects of four heavy metals on toxicity and feeding behavior of soft coral (*Subergorgia suberosa*). J Oceanogr Taiwan Strait 23:293–301

Perez MH, Wallace WG (2004) Differences in prey capture in grass shrimp *Palaemonetes pugio*, collected along an environmental impact gradient. Arch Environ Contam Toxicol 46:81–89

Pichavant K et al (2000) Effects of hypoxia on growth and metabolism of juvenile turbot. Aquaculture 108:103–114

Pichavant K, Person-Le-Ruyet J, Le Bayon N, Severe A, Le Roux A, Boeuf G (2001) Comparative effects of long-term hypoxia on growth, feeding and oxygen consumption in juvenile turbot and European sea bass. J Fish Biol 59:875–883

Pihl L, Baden SP, Diaz RJ, Schaffner LC (1992) Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. Mar Biol 112:349–361

Reichmuth JM, Roudez R, Glover T, Weis JS (2009) Differences in prey capture behavior in populations of blue crab (*Callinectes sapidus* Rathbun) from contaminated and clean estuaries in New Jersey. Estuar Coast 32:298–308

Rice SD, Short JW, Stickle WB (1989) Uptake and catabolism of tributyltin by blue crabs fed TBT contaminated prey. Mar Environ Res 27:137–145

Rubenstein NI (1979) A benthic bioassay using time-lapse photography to measure the effect of toxicants on the feeding behavior of lugworms (Polychaeta: Arenicolidae). In: Vernberg WB, Thurberg FP, Calabrese A, Vernberg FJ (eds) Marine pollution: functional responses. Academic Press, New York, pp 341–351

Sagasti A, Schaffner LC, Duffy JE (2001) Effects of periodic hypoxia on mortality, feeding and predation in an estuarine epifaunal community. J Exp Mar Biol Ecol 258:257–283

Santos MH, da Cunha N, Bianchini A (2000) Effects of copper and zinc on growth, feeding and oxygen consumption of *Farfantepenaeus paulensis* postlarvae (Decapoda: Penaeidae). J Exp Mar Biol Ecol 247:233–242

Sarojini R, Reddy PS, Nagabhushanam R (1992) Acute and chronic tributyltin-induced alterations in digestive enzymes of the prawn, *Caridina rajadhari*. Uttar Pradesh. J Zool 12:20–24

Sastry KV, Gupta PK (1979) The effect of cadmium on the digestive system of the teleost fish, *Heteropneustes fossilis*. Environ Res 19:221–230

Scarlett A, Galloway TS, Canty M, Smith EL, Nilsson J, Rowland SJ (2005) Comparative toxicity of two oil dispersants, Superdispersant 25 and Corexit 9527, to a range of coastal species. Environ Toxicol Chem 24:1219–1227

Schweitzer LE, Bay SM, Suffet IH (2000) Dietary assimilation of a polychlorinated biphenyl in adult sea urchins (*Lytechinus pictus*) and maternal transfer to their offspring. Environ Toxicol Chem 19:1919–1924

Seebaugh DR (2010) Relationships between pollutant-induced digestive toxicity and the assimilation and subcellular partitioning of elements by grass shrimp *Palaemonetes pugio*. PhD dissertation, City University of New York, New York

Seebaugh DR, Wallace WG (2004) Importance of metal-binding proteins in the partitioning of Cd and Zn as trophically available metal (TAM) in the brine shrimp *Artemia franciscana*. Mar Ecol Prog Ser 272:215–230

Seebaugh DR, Estephan A, Wallace WG (2006) Relationship between cadmium assimilation by grass shrimp (*Palaemonetes pugio*) and trophically available cadmium in amphipod (*Gammarus lawrencianus*) prey. Bull Environ Contam Toxicol 76:16–23

Seebaugh DR, L'Amoreaux WJ, Wallace WG (2011) Digestive toxicity in grass shrimp collected along an impact gradient. Aquat Toxicol 105:609–617

Seebaugh DR, Wallace WG, L'Amoreax WJ, Stewart GM (2012a) Carbon assimilation and digestive toxicity in naïve grass shrimp (*Palaemonetes pugio*) exposed to dietary cadmium. Bull Environ Contam Toxicol 88:449–455

Seebaugh DR, Wallace WG, L'Amoreax WJ, Stewart GM (2012b) Assimilation of elements and digestion in grass shrimp pre-exposed to dietary mercury. Arch Environ Contam Toxicol 63:230–240

Seick H, Decho AW, Forbes VE (1999) Effects of chronic metal exposure and sediment organic matter on digestive absorption efficiency of cadmium by the deposit-feeding polychaete *Capitella* species. Environ Toxicol Chem 18:1289–1297

Seitz R, Marshall LS Jr, Hines AH, Clark KL (2003) Effects of hypoxia on predator–prey dynamics of the blue crab *Callinectes sapidus* and the Baltic clam *Macoma balthica* in Chesapeake Bay. Mar Ecol Prog Ser 257:179–188

Selig ER, Casey KS, Bruno JF (2012) Temperature-driven coral decline: the role of marine protected areas. Glob Chang Biol 18:1561–1570. doi:10.1111/j.1365-2486.2012.02658.x

Shipp E, Grant A (2006) *Hydrobia ulvae* feeding rates: a novel way to assess sediment toxicity. Environ Toxicol Chem 25:3246–3252

Shoji J, Masuda R, Yamashita Y, Tanaka M (2005) Predation on fish larvae by moon jellyfish *Aurelia aurita* under low dissolved oxygen concentrations. Fish Sci 71:748–753

Socci R, Farmanfarmaian A (1985) Effect of heavy metals on the intestinal absorption of L-leucine and L-methionine in the toadfish, *Opsanus tau*. In: Vernberg FJ, Thurberg FP, Calabrese A, Vernberg WB (eds) Marine pollution and physiology: recent advances. University of South Carolina Press, Columbia, pp 267–279

Stierhoff KL, Targett TE, Miller KL (2006) Ecophysiological responses of juvenile summer and winter flounder to hypoxia: experimental and modeling analyses of effects on estuarine nursery quality. Mar Ecol Prog Ser 325:255–266

Taylor EJ, Jones DP, Maund SJ, Pascoe D (1993) A new method for measuring the feeding activity of *Gammarus pulex* (L.). Chemosphere 26:1375–1381

Thetmeyer H, Waller U, Black KD, Inselmann S, Rosenthal H (2001) Growth of European sea bass (*Dicentrarchus labrax* L.) under hypoxic and oscillating oxygen conditions. Aquaculture 174:355–367

Wallace WG, Hoexum Brouwer T, Brouwer M, Lopez GR (2000) Alterations in prey capture and induction of metallothioneins in grass shrimp fed cadmium-contaminated prey. Environ Toxicol Chem 19:962–971

Wegner A, Besseling E, Foekema EM, Kamermans P, Koelmans AA (2012) Effects of nanopolystyrene on the feeding behavior of the blue mussel (*Mytilus edulis* L.). Environ Toxicol Chem 31:2490–2497

Weis JS, Khan AA (1990) Effects of mercury on the feeding behavior of the mummichog, *Fundulus heteroclitus* from a polluted habitat. Mar Environ Res 30:243–249

Weis JS, Weis P (1995) Effects of embryonic exposure to methylmercury on larval prey capture ability in the mummichog, *Fundulus heteroclitus*. Environ Toxicol Chem 14:153–156

Wiedenmann J, D'Angelo C, Smith EG, Hunt AN, Legiret F-E, Postle AD, Achterberg EP (2013) Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nat Clim Change 3:160–164

Wong CK, Chu KH, Tang KW, Tam TW, Wong LJ (1993) Effects of chromium, copper and nickel on survival and feeding behaviour of *Metapenaeus ensis* larvae and postlarvae (Decapoda: Penaeidae). Mar Environ Res 36:63–78

Zhou T, Scali R, Weis JS (2001) Effects of methylmercury on ontogeny of prey capture ability and growth in three populations of larval *Fundulus heteroclitus*. Arch Environ Contam Toxicol 41:47–54